THE PLANT KINGDOM

A TEXTBOOK
OF GENERAL BOTANY

By

WILLIAM H. BROWN

GINN AND COMPANY

BOSTON · NEW YORK · CHICAGO · LONDON · ATLANTA · DALLAS · COLUMBUS · SAN FRANCISCO

447.7

The Athenæum Press
GINN AND COMPANY · PRO-
PRIETORS · BOSTON · U.S.A.

PREFACE

In 1925 the author published a textbook of general botany, the greater part of which was "devoted to the physiology, morphology, and reproduction of seed plants." This book was small, and perhaps better adapted to a semester than to a full-year course. It was very well received: so much so, that a number of users of the book have suggested that it be enlarged to meet the requirements of a full-year course, particularly by the inclusion of an adequate treatment of the divisions of the plant kingdom.

During comparatively recent years there have been tremendous advances in our understanding of the interrelationships of various groups of plants which make it feasible to present the development of the plant kingdom in a much more interesting manner than was previously possible. A comparatively small part of this new understanding is reflected in modern texts. It would seem, therefore, that there should be a real place for a textbook in which the newer knowledge and viewpoints are incorporated in such a way as to make them readily understood and easily remembered.

The new information not only makes the plant kingdom more interesting but makes it possible to group plants in such a way that the remembering of their structures and life histories is greatly facilitated. When, as is the prevailing custom in textbooks, the direction of evolution in the green algae is illustrated by such heterogeneous mixtures as *Protococcus*, *Ulothrix*, *Spirogyra*, *Oedogonium*, and *Vaucheria*, it is no wonder if students find it difficult to remember the contrasting details, or if they fail to be greatly impressed by the use of these forms as a proof of an evolutionary process.

Ample illustrations are a great help in the study of plants. The use of actual specimens is, of course, indispensable. In teaching, illustrations are also necessary and have essential roles for which it is impracticable to employ actual specimens. It is not possible to have available at the proper time all the desired stages of the various plants which are to be presented, and it is usually impracticable to have more than a small proportion of them. While the student may examine specimens in the laboratory or the classroom, they are, for the most part, not available for home study and review. Descriptions without figures are wholly inadequate for a real understanding. It follows that illustrations should be very ample if a student is really to understand the material presented to him in the text. In this book the various details are fully illustrated.

In teaching the plant kingdom, it was for years the custom to use what was known as a type course in which different groups were represented by types, and students were taught practically nothing more than the types. After a time it became evident that this method was unsatisfactory, as it presented only certain individual plants and not the plant kingdom; and the method has been variously modified. It is perhaps impossible and undesirable to get entirely away from the system of types, or at least representatives, because no students can learn the plant kingdom from generalities. Knowledge, after all, must be based on concrete facts; and in botany this must be obtained from more or less intimate knowledge of individual plants. The type course is confined to a few plants; it does not present intermediate forms; it gives no idea of a class as a whole; and, particularly, it does not present a true perspective of the development of the plant kingdom. It is not possible nor is it necessary to know all the types of the different groups or to have a thorough knowledge of all intermediate forms. In this book the main types have been treated at some length, while variations and the principal characters of intermediate forms have been discussed much more briefly, often without the mention of names. For showing a range of forms, reliance has been placed largely on illustrations from which students may be expected to absorb more ideas or to get a much more correct impression than would be possible from a short and inadequate description.

The amount of material for which students should be held responsible will naturally vary with the length of the course, the previous preparation of the student, and various other factors.

A casual comparison of modern texts of chemistry and physics with those of botany gives the impression that those of botany are rather shorter than the others, and the experience of the author indicates that it is within the ability of the average student of botany to master all the material presented in this book. There will be those who will think it desirable to give less. In preparing this text the author has had these in mind, and also those who have expressed the desire to use it as a text for a semester's course. For this reason some of the material has been placed in small type. But it is believed that where all of the material cannot be given, the presence of the material in small type will be very useful. Considerable effort has been expended to see that the text reads as a connected whole whether with or without the material in small print. In giving courses in botany, it is a very general practice of professors to expand the material in the text and to make liberal use of illustrations and illustrated material. While no text can entirely replace this valuable contribution, it must be said that the ideas which students get are often imperfect and fleeting. The material in small print has much the same relation to that in large type as a professor's lecture has to an average shorter text. A student who reads it, even though he does not remember the details, will have a much clearer idea of the subject; just as he would after listening to a professor's explanation. It can be used in various ways. The material could be required of students on daily or weekly quizzes, but not on final examinations. A student might be required to read it and to show that he has done so by having a general idea of its content; or he could be simply advised that a perusal of it would add greatly to his understanding of the subject.

The development of the colonial *Volvocales* affords a good example of how small-type material may be used. Most texts mention only one or two members of this series. Unless this is supplemented in some way, it is hard to see how a student can have any real idea of how beautiful and complete an evolutionary series there is in the *Volvocales*. In this text the initial member, *Chlamydomonas*, and the highest type, *Volvox*, are treated in large type, and with these descriptions goes a brief statement as to evolution from the one to the other, with reference to figures of intermediate types. Intermediate members are described in small type and are illustrated in figures. A student who reads the small type and examines the figures should have a good background for an understanding of the evolution of motile colonies even though he does not remember the names of any of the individual forms or exactly how various characters are combined in any of the individual species.

Facts in themselves are likely to be dry and uninviting, and are never so interesting and stimulating as the ideas, thought, and reasoning which are based on them. When botanists had only a very hazy idea as to the relation of the members of such a group as the green algae and were groping for a logical system of classification, it was naturally very difficult to present the subject in a way that would be interesting and would stimulate thought and reasoning. With a clearer view as to relationship it is very much simpler to direct the thoughts of students in such a way as to develop their powers of reasoning and enable them to see system and order in the plant kingdom. In most textbooks of botany discussions of relationship and the tracing of evolution are either practically omitted or given very brief consideration. In this book an attempt has been made to increase the interest of the students and to stimulate their reasoning by discussion, particularly of how groups of plants are related one to the other and of the different courses which evolution has taken.

In various places in the text it is shown that our knowledge is incomplete and that in some cases different authorities place various interpretations on the known facts. Any confusion which may result in the mind of the student will be more than offset by the truer perspective that this method should give. Controversial subjects are usually discussed in small type.

Very considerable care has been taken with the illustrations. If a student is expected to develop his powers of observation or to make accurate drawings, those in his text should be of the best quality. A large number of illustrations dealing with the divisions of the plant kingdom have been taken from the original writings of botanists of high standing. Most of them have been redrawn; this has been necessary for the sake of clearness, as original illustrations are often in colors, or are reproduced in some such style, or are of such a size, as not to be suitable for direct reproduction in a text. The word "After" is used to indicate an illustration redrawn from the original source. In a few cases drawings have been modified to allow for such obvious things as shrinkage of protoplasm, or made slightly diagrammatic in order that they might be more understandable. Except where such facts are noted, the reproductions are as near like the originals as it has been feasible to have them made. In reproducing a few of the reconstructions from fossils, slight liberties have been taken with such things as shading.

More than half of the illustrations in this book are drawings made especially for it. The others are taken from "A Textbook of General Botany." In that book acknowledgment is made to all those who assisted me in the making of the drawings. I take this occasion, however, to express my thanks again to the following who were my students at the time they made very excellent drawings for that text and who are now on the staffs of various institutions of learning: Dr. José K. Santos drew Figs. 10, 13, 19, 28, 39, 40, 41, 43, 48, 50, 58, 126, 143, 144, 164, 165, 166, 197, 198, 200, 203, 225, 227, 230, 324, 362, 379, 380, 382; Dr. Maria Pastrana Castrense, Figs. 42, 55, 56, 57, 59, 73, 74, 82, 92, 103, 106, 107, 130, 149, 151, 157, 158, 161, 162, 207, 208, 209, 221, 226, 228, 231, 232, 240, 285, 333, 342, 345, 347, 352, 356, 357, 358, 360, 361, 367, 389, 418, 419, 432, 444, 504, 508, 516, 517, 525 (left), 566, 570, 584, 742, 743, 761, 781, 934; Professor Maria B. Gutierrez, Figs. 22, 26, 27, 30, 32, 47, 53, 61, 72, 79, 96, 114 (left), 115, 128, 167 (right), 168, 169, 170, 171, 220, 284, 289, 323, 327, 329, 332, 337, 660, 670, 696, 803 (left), 804; Mr. Gregorio T. Velasquez, Figs. 112, 790, 794, 795, 897, 997, 999, 1004 (right), 1005; Mr. Edilberto Karganilla, Figs. 34, 36, 46, 98, 105, 420, 544 (left); Mrs. Maria Tolentino Vallarta, Figs. 14, 310, 681, 763, 812, 814, 815, 817; Mr. Juan Pascasio, Figs. 159, 363, 368, 816, 842; Miss Ursula Uichanco, Fig. 824.

I wish here to express my indebtedness for photographs to Dr. William S. Copper, Dr. Forest Shreve, Dr. George E. Nichols, Professor D. A. Herbert, Dr. George H. Shull, Mr. Frederick V. Coville, Dr. W. W. Garner and Mr. H. A. Allard, Dr. H. Otley Beyer, Dr. H. H. Bartlett, Dr. C. Skottsberg, and the Bureau of Science, Manila.

I am particularly indebted to Dr. José K. Santos, head of the Department of Botany, University of the Philippines, whose encouragement was really responsible for my undertaking the preparation of the book. Dr. Santos has been of great assistance in many respects, particularly in the furnishing of various materials for illustrations and in the making of illustrations. Dr. Santos suggested the inclusion of Figs. 325, 326, and 328, and made the drawings for them. He also suggested the inclusion of Figs. 17 and 127 and designed the illustrations.

I am also greatly indebted to Dr. Joaquin Marañon for very valuable suggestions and criticisms in the preparation of the text.

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CHAPTER I

INTRODUCTION

Botany is the science which deals with plants. Science may be defined as knowledge which is generally accepted because it has been proved to be true and which has been classified and arranged so as to demonstrate general truths or the operation of natural laws.

The aim of botany is not, therefore, the accumulation of isolated facts, but to demonstrate the general laws which underlie the development, composition, and activities of the plant world. In its broadest sense, botany may be said to include all the systematized knowledge of plants. The field covered by botany is so extensive that no man can hope to be intimately acquainted with all its branches, and so botanists usually work in a limited part of the field. Botany is often divided into a number of subordinate sciences such as systematic botany (the classification of plants according to their relationships), morphology (the structure of the different parts of plants), physiology (the functions of plant organs), plant geography (the distribution of plants), genetics (which deals with inheritance and variation), and applied botany, which embraces agriculture, horticulture, forestry, pharmacognosy, bacteriology, plant pathology, etc.

The study of botany is useful for its general educational value as well as for its practical applications. Plants are probably the most conspicuous elements in the natural environment of most people, and it is through plants that a large part of the human race comes most frequently in contact with nature. The cultural value of botanical study is very great. Plants are living things, and in them we can conveniently study many of the natural laws which deal with life. Plants are wonderful objects for observation and experimentation. A study of the development of plants through the ages, their intricate structure, and their wonderful adjustment to their surroundings affords great intellectual delight. Perhaps the greatest advantage of botanical study is the development of the student himself. The study of botany is particularly useful in developing powers of observation and is most valuable in giving students scientific methods of thought. The student has excellent opportunities for making scientific observation and drawing conclusions along scientific lines. Such training is most useful in dealing with the affairs of life.

The practical uses of botany and the applications which one may make of them are very diverse and far-reaching. The food of all animals, including man, comes from plants, either directly or through other animals. Plants furnish us much of the material from which our clothes are made. They also supply us with the wood that we use for fuel, for making furniture, for building houses, and for many other purposes. They furnish us with numberless valuable products, such as many kinds of medicine, perfumes, paper, etc. In breathing, animals take in oxygen. This is combined with carbon, forming carbon dioxide, which is exhaled. All the available oxygen would soon be exhausted, and all animals exterminated, if it were not for the fact that plants take in carbon dioxide, utilize the carbon, and liberate the oxygen.

Even the remains of plants that have long been dead are useful to man. Among these is coal, which is used for fuel, and which also yields gas, coke, and coal tar. The last named is the basis of the synthetic-dye industry and the source of many valuable medicines and other useful products.

As human life is so intimately connected with plants and dependent upon them, it is only natural that botany should be a subject of great interest; and it would seem that all educated persons should have some knowledge of it, if only for the purpose of understanding better so important a part of their environment as the vegetable kingdom. Such knowledge can hardly fail to give one a keener appreciation and enjoyment of nature.

While botany has great cultural value, the science is even more important on account of its useful applications. The applied branches, which are sometimes known as economic botany, are the most practical parts of the subject, but the theoretical branches also are useful. Although some of the applied branches, such as agriculture, horticulture, and forestry, have long since been separated from the parent science, their scientific application is dependent upon a knowledge of the fundamental principles of botany, and these applied branches have been continually improved by the employment of new principles discovered in the more theoretical fields. A knowledge of botany is useful not only to those engaged in the applied branches but also to everyone in daily life. It teaches us the values of different kinds of food and enables us to understand and control such processes as the spoiling of food, the decay of wood, the contamination of water supplies, and the molding of leather. Many uses will be evident as the student acquires familiarity with the subject.

CHAPTER II

THE PLANT AND ITS ENVIRONMENT

The plant. All living organisms are grouped into two kingdoms, the animal kingdom and the plant kingdom. The members of these two kingdoms are very similar in their fundamental constitution and vital processes. Plants, like animals, are living and breathing organisms characterized by growth and reproduction.

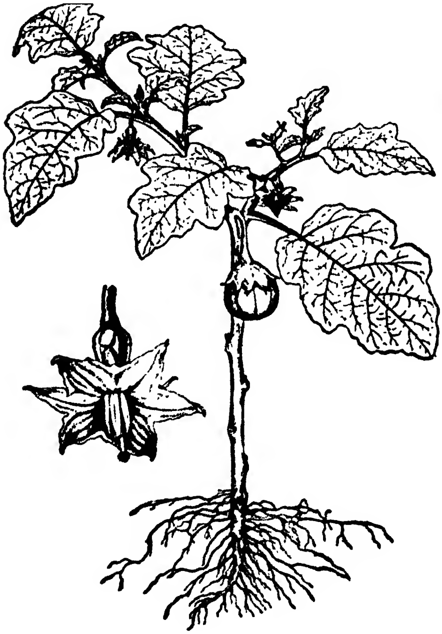

FIG. 1. An eggplant with roots, stem, leaves, flowers, and fruit. (Plant × ⅙, single flower × ⅔)

Like animals, plants range in size from very large species to minute ones that can be seen only with the aid of a microscope. In dealing with the larger and more conspicuous kinds it is very easy to tell whether a given organism is an animal or a plant. This, however, is not the case with all small species, and there are whole groups of organisms which have been regarded by zoologists as animals and by botanists as plants. At this place it would therefore be difficult to give an understandable definition that would include all plants and exclude all animals.

Plants not only vary from very minute species to trees which reach tremendous heights, but are also very diverse in shape and structure. The small ones are very different in form from the average person's conception of plants (Fig. 468). Many of the minute plants that live in water have slender projections known as flagella (Fig. 444) which enable them to swim rather rapidly for their size. As the larger and more complex plants are the ones that are most familiar and most conspicuous, the first part of this book will be devoted to them. The typical higher plant is an organism with roots, flowers, leaves, one or more stems, and roots. Fig. 1 represents these various parts in the case of an eggplant. Except where other plants are specifically mentioned, statements in the first part of this book will refer to these higher or flowering plants.

Leaves. The green color, which is due to the presence of a green coloring matter called *chlorophyll,* is one of the most important characteristics of the typical higher plant. Chlorophyll, in the presence of sunlight, enables the plant to manufacture sugar from carbon dioxide (a gas found in the air) and water (obtained from the soil). The sugar is the starting point from which all the complex chemical compounds found in the plant are built. The roots of the plant take from the soil not only water but, in addition, simple chemical compounds which are also used in the elaboration of the more complex and important plant materials. The manufacture of sugar from carbon dioxide and water is the chief function of the leaves of a plant. This process is known as *photosynthesis.*

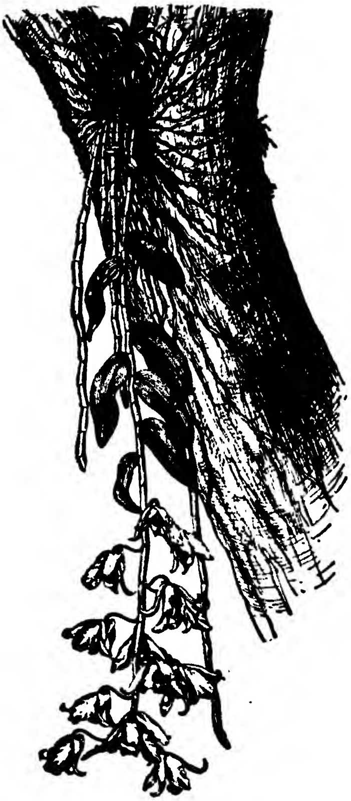

FIG. 2. A tropical orchid (*Dendrobium anosmum*), attached by means of its roots to the trunk of a tree. ($\times \frac{1}{8}$)

Animals do not possess chlorophyll and are unable to build up their food substances from carbon dioxide, water, and simple mineral salts, but are dependent upon plants for food which has already been elaborated. Plants can and usually do remain in one place, where they absorb all the substances which they require. Animals, on the other hand, must either move about in search of food or, as is the case with many marine animals whose food comes to them in the water, have it brought to them. This difference in the method of obtaining food appears to be responsible for many of the distinctions between the more complex plants and animals.

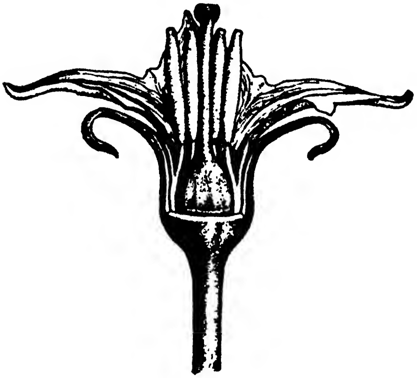

FIG. 3. A flower of an eggplant, split to show parts. (× 1½)

Roots. The roots of most plants are in the ground, although there are many plants, particularly in the tropics, which grow on other plants or on rocks and have their roots in the air (Fig. 2). The chief functions of the roots are to absorb water and mineral matter and to hold or anchor the plant in place.

Stems. The stem serves as a support for the leaves, flowers, and fruits; for the transport of water and mineral matter from the roots to the leaves and other organs; and for conducting manufactured food from the leaves to other parts of the plant.

Flowers. In the flowers, male and female elements unite in sexual reproduction, a process which is very similar in both plants and animals. This process in plants is dependent on the transfer of small usually yellow grains called *pollen* from sacs known as *anthers* to the *pistils*, which contain the female elements known as *eggs*. The pollen is in many cases transferred by wind, or by insects which are attracted by the color or odor of the flowers.

The various parts of the flower of an eggplant are shown in Fig. 3. In the drawing the flower is represented as split down one side to show the different organs. The conspicuous expanded part is the *corolla.* In the center is the *pistil,* composed of a basal portion (the *ovary*), a terminal portion (the *stigma*), and a slender structure (the *style*), which connects the ovary and the stigma. Around the pistil are the *stamens,* which consist of slender *filaments* and large terminal *anthers.* Below the corolla is the *calyx* with pointed green lobes. The calyx enclosed the remainder of the flower when it was a bud. In many flowering plants the flowers are so inconspicuous that many people regard the plants as lacking flowers.

The process by which the male element is carried to the egg is shown diagrammatically in Fig. 4. In this figure are seen four anthers, three of which have opened so that the pollen grains are visible. When the pollen grains are deposited on the stigma, they produce long tubes which grow down into the ovary and enter small oval bodies, the *ovules,* each of which contains an egg. In Fig. 4 the pistil is represented as cut in half longitudinally. In the cavity in the ovary are shown six ovules. There are four *pollen tubes* in the pistil. The longest of these is seen entering an ovule.

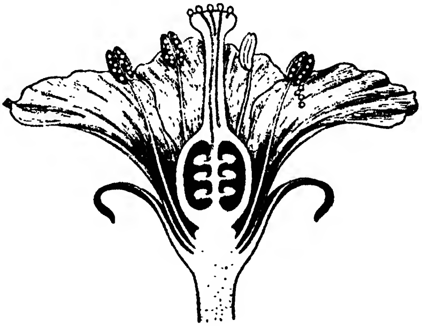

FIG. 4. Diagram of a section of a flower at the time of fertilization

Fruits. The male element escapes from the end of the pollen tube and fuses with the egg, after which the product of this fusion develops and becomes an *embryo,* the ovule being transformed into a *seed.* The seeds are inclosed in the *fruit,* which is the ripened ovary. When the seed meets with conditions favorable for development, the embryo grows and becomes an independent plant. The fruit not only contains the seeds but frequently serves as a means of distributing them to distant places where they may find favorable conditions for development. Examples are seen when a bird eats a fleshy fruit and later deposits the seeds at a considerable distance, or when the husk of the coconut (Fig. 389) enables the seed to float to a new locality.

All parts of the plant have separate functions, but all contribute to what, after all, is the main function of the plant, the production of offspring. The success of the plant, if we look at it from the standpoint of the plant itself, depends not on its size or beauty but on its power to reproduce its kind and occupy territory. The leaves contribute toward this end by manufacturing food used in the seed; the stems, by giving support to the leaves and reproductive structures; the roots, by absorbing water and mineral matter and anchoring the plant in place; and the flowers, by producing the seed.

Environment. We have seen that a typical higher plant is an organism with leaves, stems, flowers, and fruits, all of which are in the air, and roots, which usually grow in the soil. In discussing the environment of a plant, therefore, we have to consider the component parts of the air and of the soil.

Air. The air is a mixture of gases. The principal gases in this mixture are colorless, tasteless, and odorless, so that we cannot see, taste, or smell them. The principal gases of the atmosphere are nitrogen, oxygen, carbon dioxide, and water vapor. Nitrogen constitutes about four fifths of the air, and oxygen about one fifth. Carbon dioxide is always present in small quantities (about .03 per cent), while water vapor occurs in varying quantities, depending on the circumstances.

In respiration (breathing), plants and animals take in oxygen; without it they could not carry on respiration and so would soon die. Respiration is performed in all the living parts of plants and is just as important for plants as for animals. We can see this readily in the case of seeds, which, if deprived of oxygen, will not germinate.

Carbon dioxide, as we have seen, is used by plants for the manufacture of sugar.

The water vapor in the air is also an important factor in the environment of plants. The principal constituent of the living parts of plants is water, and plants expose moist surfaces to the air. When water or a moist surface is exposed to the air, some of the water is changed to water vapor and mixes with the air. This process is known as evaporation. If a small amount of water is left in an uncovered glass, we know that the water evaporates and leaves the glass dry. We also see the result of evaporation when we dry wet clothes. The rate of evaporation depends in part on the amount of water vapor in the air. We are familiar with the fact that when the air is wet it takes much longer for anything to dry than it does when the air is dry. In other words, as the amount of water vapor in the air increases the rate of evaporation decreases, because moist air will take up less water than will dry air. The moist surfaces of plants, like any other moist surfaces, lose water by evaporation. The evaporation of water from plants is known as *transpiration*; it is a very important process from the standpoint of the plant, and one that we shall examine in considerable detail in a later chapter. The rate of transpiration will naturally be influenced by the amount of water vapor in the air, the rate decreasing as the quantity of water vapor in the atmosphere increases. If a plant continues to lose water faster by transpiration than it can obtain it from the soil, the plant will wilt and finally die. It is for this reason that many delicate plants cannot be grown in places where the air is very dry, as they would dry up and die from excessive loss of water. The amount of water vapor in the air is not the only factor which affects the rate of evaporation, as the rate is increased by wind, heat, and light.

Soil. The soil is composed of small rock particles mixed with varying quantities of decaying organic matter. Between the particles are spaces which usually contain air. The air in these spaces is very essential to plants, as it contains oxygen which enables the roots to carry on respiration.

The soil particles are surrounded by thin films of water. The roots of plants absorb water from these films. In very wet soil the spaces between the soil particles may be filled with water. This is a very bad condition for most crops, as the water keeps the air out of the spaces and the soil then contains too little oxygen for the roots of most plants.

The soil particles are composed of a number of different compounds. Small quantities of these go into solution in the water around the particles and pass into the roots of plants. The elements which are necessary for plants in general and which are obtained from the soil are nitrogen, phosphorus, sulfur, calcium, iron, potassium, and magnesium, with extremely small quantities of some others such as manganese.

The elements oxygen, hydrogen, and carbon are very important constituents of plants. Hydrogen is obtained from water, oxygen from both water and the air, and carbon from the carbon dioxide in the air. The other elements needed by plants are taken from the soil.

Habit and habitat. There are many different environments in which plants grow, and in each case the plants are fitted by their structure for their particular environment. The kind of environment in which a plant grows naturally is known as its habitat, while the form of the plant is spoken of as its habit.

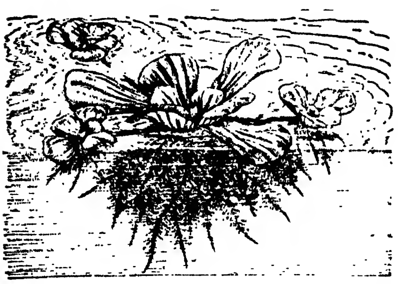

FIG. 5. A floating aquatic plant (*Pistia stratiotes*) that is found in the tropical and subtropical regions of both hemispheres. (× ½)

Terrestrial, aquatic, and epiphytic plants. Plants that grow in the ground, as is the case with most of the higher plants, are *terrestrial* plants. Those that have their habitat in water are known as *aquatic* plants, or *aquatics* (Figs. 5, 97, 311). If they are submerged in the water, they are *submerged aquatics*. Those that grow perched on other plants but obtain no nourishment from the plants on which they grow are *epiphytic* plants, or *epiphytes* (Figs. 2, 104, 233, 252, 255, 271, 272). In cold temperate regions the epiphytes are mosses and mosslike plants and lichens. In warmer regions, particularly in the moist tropics, many flowering plants also grow as epiphytes. Some of the most beautiful of the orchids belong to this class (Fig. 2). Epiphytes are dependent for their water supply on rain and on water which condenses from the atmosphere.

Xerophytes, mesophytes, and hydrophytes. Plants that are fitted for growing in a dry habitat are known as *xerophytes* (Figs. 276–279). The cacti are good examples (Fig. 277). These plants have enlarged stems in which they store water for use when a sufficient supply is not available from the ground. Plants, such as aquatics, which can grow only under very wet conditions are *hydrophytes*. Most plants are not specialized to grow in either very

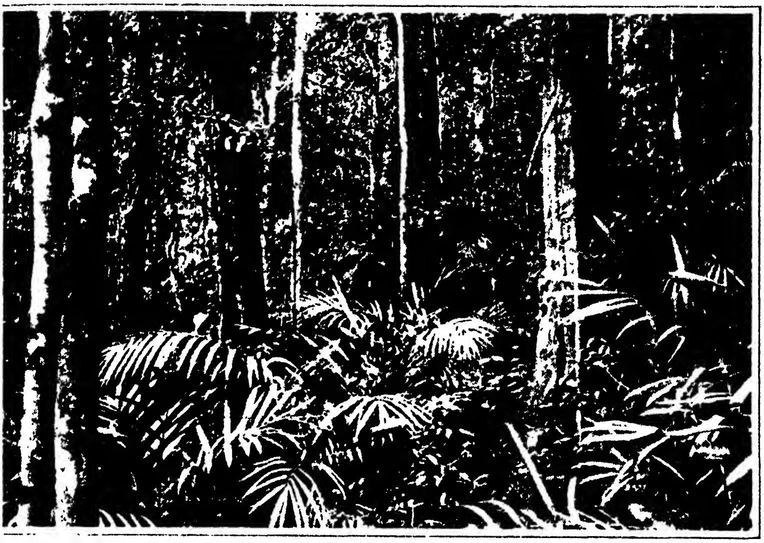

FIG. 6. A mesophytic tropical forest (Philippine)

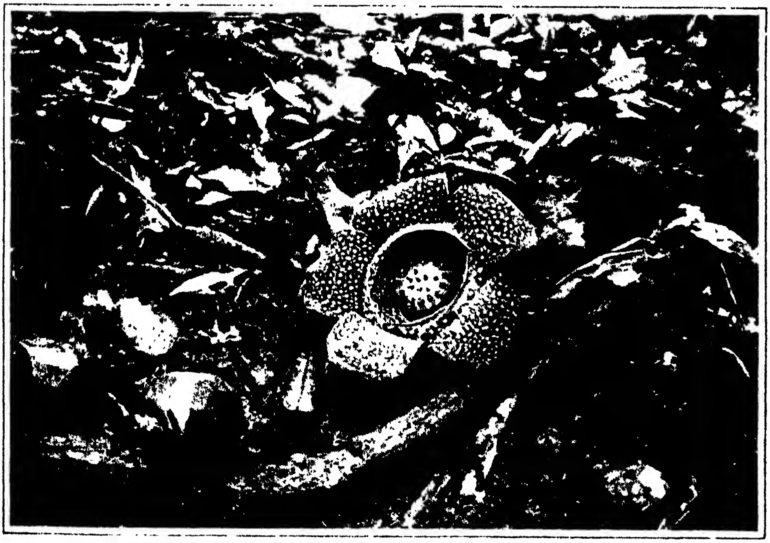

FIG. 7. Flower and buds of *Rafflesia manillana*, a true parasite on the roots of a *Cissus* vine

Rafflesia has no regular leaves or stem, the flowers growing directly from the roots of the host. Another species of *Rafflesia*, *R. arnoldi*, has the largest known flowers, these being about a meter in diameter dry or very wet habitats, but thrive under conditions intermediate between these two extremes (Fig. 6). Such plants are *mesophytes*; they include the great majority of cultivated plants, such as beans, tomatoes, corn, squashes, etc.

Parasites and saprophytes. While most plants manufacture their own food, there are many which live on food that has already been elaborated. Those plants that send absorbing organs into living plants from which they draw their nourishment are *parasites* (Figs. 7, 189, 60). As true parasites do not contain chlorophyll with which to manufacture the food they require, they do not have the green color of chlorophyll. Some plants, however, have absorbing organs by means of which they obtain materials from other plants, and at the same time possess chlorophyll which enables them to manufacture food. Such plants are *hemiparasites*, of which the mistletoe is a good example (Fig. 8).

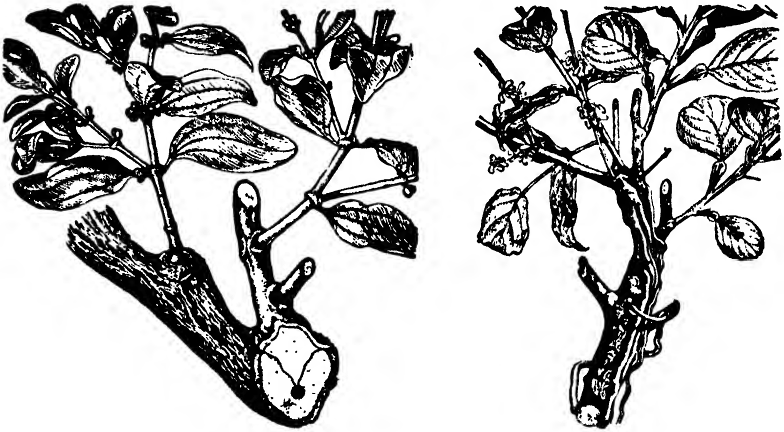

FIG. 8. Two species of tropical mistletoe which are hemiparasites

Left, *Viscum orientale*, the root of which forms a single haustorium (absorbing organ). Right, *Loranthus philippensis*, the roots of which grow on the surface of the host and send many haustoria into it

Another class of plants, instead of manufacturing their food, absorb it from decaying organic matter. These are *saprophytes*. Numerous saprophytic flowering plants obtain their food from decomposing organic matter in the soil (Fig. 9). These, like the parasites, lack chlorophyll and are frequently colorless; they may have various colors, but they never have the green color of chlorophyll. The most numerous of the parasites and saprophytes belong to the lower groups of plants. Most of the bacteria and all of the fungi either are parasitic on plants or animals or are saprophytic.

Annuals, biennials, and perennials. According to the length of time they live, plants are designated as annuals, biennials, and perennials. Those that live for only one year or a single season are *annuals*; these include our cereals, such as corn, rice, and wheat, and many of our vegetables, such as tomatoes, cucumbers, etc.

Biennials are plants that live during the favorable growing periods of two years, and produce seeds and die during the second year. Biennials are rather numerous in temperate zones, and include such common vegetables as beets, carrots, and cabbages.

Plants like roses and cannas that live from year to year or through a series of years are *perennials*.

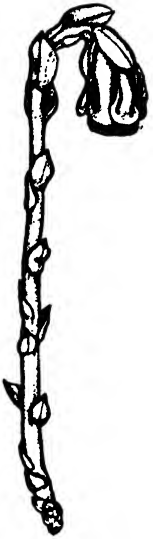

FIG. 9. *Monotropa* (Indian pipe), a saprophyte with colorless leaves (× ⅔)

NAMES OF PLANTS

Species. In dealing with the very large number of plants that occur in the world it is necessary not only to have names for the various species but also to have a system of classification that groups plants together according to their similarities and relationships. The different kinds of plants are regarded as different species, and each kind is given a species name, or specific name. The structure of the flower is the most important criterion in the classification of flowering plants.

Groups of plants. In classifying plants the different kinds (*species*) are grouped into genera, families, orders, classes, and divisions. The whole plant kingdom is divided into *divisions*, one of which, the *Spermatophyta*, includes all seed plants. Divisions are subdivided into *classes*. The classes of the *Spermatophyta* are gymnosperms (seed plants without flowers in the popular sense) and angiosperms (flowering plants). The monocotyledons and dicotyledons are subclasses of the flowering plants. An *order* is a large group which includes plants that have some prominent characteristics in common and show a natural relationship to each other. An order includes one or more related families. A *family* is therefore a subdivision of an order and consists of a group of closely related genera, although a family may contain only a single genus if this genus is distinct enough from all others to be put into a separate family. Usually, however, there are a number of genera in each family. A *genus* is commonly a group of closely related species, but may contain only a single species. A *species* represents a single kind of plant, the individuals of which differ from each other only in minor characters which are bridged over by intermediate forms, and in characters which are due to age, sex, nutrition, individual peculiarity or accidents, or selective breeding by man. The individuals of a species may be cross-pollinated and reproduce the same kind of plant.

Names. The species, genus, family, and order have each a separate name. In writing the name of a plant we use the generic and the specific name. The generic name is written first and then the specific name. The generic name always begins with a capital letter. In a practice which has been very much used, a specific name is always begun with a small letter. Most botanists, however, prefer to begin the specific name with a capital letter if that name is derived from the name of a person. When the specific name is not derived from a proper noun, it always begins with a small letter. As an example we may take the coconut, which belongs to the genus *Cocos* and has the specific name *nucifera*. We write first the name *Cocos* and begin it with a capital *C*. This is followed by the name *nucifera* (meaning "nut-bearing"), which is begun with a small *n*. The name is therefore written *Cocos nucifera*. As another example we may take the cultivated coleus. This plant belongs to the genus *Coleus* and has the specific name *blumei*. In accordance with a widely accepted usage the name has been written *Coleus blumei*. The name *blumei* was given in honor of the Dutch botanist Blume. Owing to the derivation of the name, most botanists prefer to write it *Blumei*. Specific names frequently refer to some character of the plant, as *nucifera* (nut-bearing), *odorata* (fragrant), *microphylla* (small-leaved), *pinnata* (pinnate-leaved). In other cases the name may be derived from a country, as *americana*; or from the name of a man, as *blumei*; or from one of various other sources. Generic names are similarly derived.

The idea "an unidentified species of the genus *Agave*" is expressed in the abbreviated form "*Agave* sp."; "several species of *Agave*" by "*Agave* spp."

Generic name. The generic name is regarded as a proper noun and is applied to only one genus in the whole plant kingdom. It is therefore begun with a capital letter. The specific name is not a proper noun and may be applied to a single species in each of any number of different genera.

Specific name. Owing to the fact that the specific name may be applied to a large number of species in different genera, the specific name is never correctly used except in connection with the generic name. The generic name, on the other hand, may be used alone, as it applies to only one genus. As an example we may take the case of the cannas. These plants belong to the genus *Canna*, so that when we use the generic name *Canna* it has a definite meaning, as we know at once that it applies to the cannas. One of the wild cannas is called *Canna indica.* If we were to use the word *indica* alone, it would not have any definite meaning, as other species in different genera are also named *indica.*

Authority for name. When the name of a plant is written for exact scientific determination, it is customary to place after it the name, or an abbreviation of the name, of the man who gave the specific name to the plant. The name *Cocos nucifera* was given by Linnæus, who is regarded as the father of systematic botany. His name is usually abbreviated L. or Linn. When exactness is required, the name of the coconut should be written *Cocos nucifera* L. or *Cocos nucifera* Linn. The necessity for this arises from the fact that in the development of botanical classification the same name has been applied by different authors to different plants.

Advantages of scientific names. The use of scientific names is necessary in order to have names that will be generally understood in all languages, because in different languages the same plant usually has different names. Also, the use of scientific names prevents confusion even in the same language, as in different regions the same common name may be applied to different kinds of plants, or the same plant may be known by different names. A very good example is the word *corn*. It may mean any small, hard seed, as that of the apple, coffee, or any one of the cereals, as wheat or rye. The name *corn* is also used specifically for an important cereal crop of a given region. In England it is applied to wheat, in Scotland and Ireland to oats, and in the United States to Indian corn, or maize. It will be seen that one common name may mean different things to different people, whereas the scientific name of Indian corn, which is *Zea mays*, has the same meaning to any botanist, no matter where he may be.

Advantages of two names. The use of two names has many advantages. The generic name signifies the group to which the plant belongs, and the specific name the individual kind of plant. When the two are used together, we immediately know the individual plant, and we also have an idea as to what are its closest relatives. Another important point is that it would be very difficult to find a sufficient number of names to enable us to give a different and appropriate one to each species. Genera are much less numerous than species, so it is not so difficult to get enough names for the genera. The use of the same specific name in many genera makes it much easier to find a sufficient number of appropriate names for the different species.

The earliest books on the classification of plants in which our modern system of names was used were written in the Latin language, and at the present time it is customary to write generic and specific names with Latin endings. For this reason they are regarded as foreign words and so are printed in italics in scientific books and articles. This method has the advantage of making the names more prominent and shows at a glance what plants are discussed in any paragraph.

People often think that the scientific names of plants are hard to remember. As a matter of fact the difficulty does not lie in the names themselves but in the fact that they are unfamiliar. Scientific botanical names become just as simple as any other names after we have heard them a few times and they have lost their strangeness. Certainly, botanical names are no more difficult than many names such as carburetor, camouflage, and superheterodyne, which have been recently introduced into the English language and are familiar to all. As a matter of fact a very large proportion of botanical names are short and simple. The botanical names of a great many familiar plants are simply the names by which these plants were known to the Romans, and many of them are very much like English common names. As an example, the rose is *Rosa*; pine is *Pinus*. Anyone who looks at scientific botanical names without prejudice will find no difficulty in mastering them.

CHAPTER III

THE CELL

When a portion of a plant is examined under a microscope, it is found to consist of a number of small boxlike compartments called *cells*. A typical plant cell is shown in Fig. 10, and a section of a group of cells in Fig. 11. A plant cell is surrounded by a firm wall called a *cell wall*, which may be regarded as a container in which the *protoplasm*, or living part of the cell, is found. Cells may be thought of as the fundamental units of all living things, whether plants or animals. The cell is the smallest unit of living matter capable of continuous independent existence and of reproduction. Very small plants or animals may consist of only a single cell, while large individuals are composed of a great many cells. An egg of either a plant or an animal is a single cell, which, by division and growth, develops into a mature individual of its species. In highly developed plants and animals cells become specialized for different uses. Thus, ordinary green plants have some cells especially suited to the absorption of water; others, to the conduction of water; and still others, to the manufacture of sugar from carbon dioxide and water. The special characters of many kinds of cells will be evident after a study of the parts of a plant. All living cells are alike, however, in their fundamental characteristics.

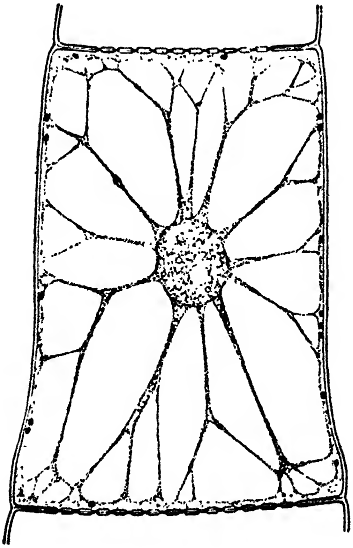

Fig. 10. A typical cell from a hair of a squash plant. (× 180)

Cell walls. Cell walls are important not only because they serve as containers of the protoplasm but also because they enable the plant to assume a definite shape. If it were not for the cell wall the protoplasm, being liquid or semiliquid, would simply spread out on the ground, as would any other liquid. The heartwood of trees consists largely of thickened cell walls of dead cells (Fig. 146). If a piece of wood is examined under a microscope, the walls of the individual cells can be readily seen. The cell wall is typically composed of *cellulose*, which is a chemical compound having the formula $(C_6H_{10}O_5)_n$ and belonging to the group of organic compounds known as carbohydrates. Cellulose is hard and colorless, absorbs water readily, and is insoluble in water. Cotton and filter paper are very good examples of nearly pure cellulose. Cellulose is well suited to the formation of cell walls, because it is rather hard and strong and because water can pass through it. Owing to its hardness and strength it gives firmness and strength to the cell wall. Since water is one of the essential constituents of plant cells, it is of great importance that the cell wall should be of some substance through which water can pass, so that water can readily enter a cell or pass from cell to cell.

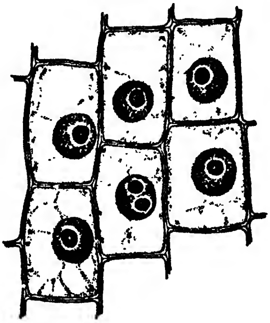
FIG. 11. A section of a group of cells from an onion root tip. (× 600)

As a constituent of wood and of fibers such as cotton, linen, etc. cellulose has always been of great value to man. Within recent years cellulose as a chemical substance has come into great prominence in the manufacture of such articles as cellophane, rayon, cellulose lacquers, high explosives, etc.

Cells that are specialized for certain purposes sometimes have in the cell wall other substances in addition to the cellulose. Cell walls that are considerably thickened, so as to give great strength, frequently contain a substance known as *lignin*. Such cells are said to be *lignified*. Wood is composed largely of lignified cells. Water passes through lignin very readily, so that the addition of lignin strengthens the wall without greatly interfering with the passage of water through it. Cells that are on the outside of plants and exposed to dry air frequently have their outside walls impregnated with a waxy substance, *cutin.* Water does not readily pass through such cell walls; consequently the walls tend to protect the cells from excessive loss of water due to evaporation. A layer of cutin is frequently found on the outside of cells that are exposed to dry air. Such a layer is known as a *cuticle.* Stems of plants are frequently protected from high rates of evaporation by the development of *cork.* The walls of cork cells also are impregnated with a waxy substance, *suberin,* which is impervious to water.

A cell can exist without a cell wall, and in some of the simpler plants, at certain times, the protoplasm escapes from the cell and surrounds itself with a new cell wall.

Animal cells do not have hard cell walls, like plants, but have a soft covering; in some cases they may be naked. For this reason the flesh of animals is soft, while the form of large animals is due to a considerable extent to their bones, and not to cell walls, as in plants.

Middle lamella. Between two adjacent cell walls there is a thin layer known as the middle lamella, which cements together the two cell walls. The middle lamella consists largely of pectose or calcium pectate. Many fruits in ripening become soft and mushy, owing largely to the disintegration of the middle lamella by the conversion of the pectose substances into pectic acid. Pectin, the material which causes apple jellies and similar fruit jellies to set, is an intermediate product between the pectose substances of the cell wall and pectic acid.

Protoplasm. Within the cell wall is found the protoplasm, or living part of the cell. The gray material in Figs. 10 and 11 is protoplasm. Protoplasm is usually a viscous liquid or a jelly. There is no sharp dividing line between these two states, and the same protoplasm may change from one to the other. The liquid state is associated with a more active condition. Protoplasm has a slightly grayish color, or it may have a yellowish tinge due to included food particles. It is usually rather transparent. Included within the protoplasm are numerous minute granules, many of which are food particles.

Protoplasm is a very complex mixture of various substances dispersed in water. Active protoplasm usually contains more than

90 per cent of water. In some cases, as in seeds, the amount of water may be much smaller, and the protoplasm becomes relatively hard. In such cases, however, the protoplasm loses most of its activity, and becomes active only when additional water is supplied. Next to water the substances which are present in greatest amount are proteins. These are very characteristic of protoplasm, and protoplasm is often said to be essentially a dispersion of proteins in water. Proteins are very complex chemical compounds with large molecules, and always contain the elements carbon, hydrogen, oxygen, and nitrogen, and frequently in addition other elements, such as sulfur and phosphorus. These last two elements are always present in the proteins of protoplasm. There are many different kinds of proteins in protoplasm. The white of an egg is a very good example of one kind of protein. Among the other organic compounds found in protoplasm are fats and carbohydrates such as sugar. Carbohydrates are compounds of carbon, hydrogen, and oxygen in which the hydrogen and oxygen are usually present in the same proportion as in water; that is, two molecules of hydrogen to one of oxygen. A considerable variety of inorganic salts are also found in protoplasm. The materials found in protoplasm will be discussed more fully in a later chapter.

Colloidal state of protoplasm. The proteins are dispersed in the water of the protoplasm as particles of colloidal size. In order to understand what is meant by a colloidal dispersion in water (sometimes called a colloidal solution) we may consider the differences between a suspension, a colloidal dispersion, and a true solution. If we were to take small particles of soil that are still large enough to be visible, and stir them in a vessel of water, they would become suspended in the water. We should then have a suspension of soil particles in water. We frequently see such a condition in muddy rivers or in agitated pools. Each soil particle is composed of many molecules. These particles would settle to the bottom if the water were to remain still for a sufficient length of time. Each soil particle could be divided into two, and we should have a suspension of smaller particles. Theoretically this process of division could be continued until each particle would consist of only a few molecules and finally of only a single one. The last condition would be a true solution, in which the individual molecules of the soil would be dispersed in water. When we put a little sugar in water, the sugar seems to disappear and to sweeten the water. In such a case we have a solution (or dispersion of molecules) of sugar in water. From the foregoing consideration it is evident that there must be every gradation between a suspension and a true solution. The condition intermediate between a true solution (dispersion of molecules) and a suspension (dispersion of visible particles) is known as a colloidal dispersion. A colloidal dispersion in water is a dispersion of particles whose size may vary between 0.1 μ and 0.001 μ. (1 μ, read "micron" or "mu," equals 0.001 millimeter.) The lower limit is regarded as the size of a large molecule, while the upper limit is slightly smaller than the smallest object of which the form can be seen with the aid of a microscope. These limits are arbitrary, as there can be no sharp division between a colloidal dispersion and a suspension. Likewise there is no sharp distinction between a colloidal dispersion and a true solution, as some complex molecules are large enough to be within the limits of size given above for colloidal particles.

A suspension is a dispersion of particles which are large enough to be visible with the aid of a microscope. A true solution is a dispersion of molecules or parts of molecules. A colloidal dispersion is a dispersion of particles which are larger than most molecules and yet too small to be seen even with the aid of a microscope.

Colloidal dispersions are not confined to dispersions of solids in liquids. Just as we may have an emulsion (which is a suspension of a liquid in another liquid, as oil in water), so we may have a colloidal dispersion of a liquid in another liquid. This condition is known as an emulsoid. Smoke is a dispersion of a solid in a gas; a cloud is a dispersion of a liquid in a gas; meerschaum is a dispersion of a gas in a solid; ruby glass is a dispersion of a solid (gold) in a solid (glass). Protoplasm is generally believed to be an emulsoid in which proteins are dispersed in water.

Importance of colloidal state. Much of the importance of the colloidal state arises from the fact that the dispersed substances have enormous surfaces for the play of surface forces and for chemical reactions. The increase in surface when a substance becomes finely divided can be illustrated by the following example:

A cubic centimeter of material in the form of a cube would have six sides, each with an area of 1 square centimeter. The cube would therefore have a surface of 6 square centimeters. If this cube were divided into two parts by a cut in a plane parallel with two sides, the surface would be increased by the area of two sides. The two parts would then have a total area of 8 square centimeters. Subdividing these parts would, of course, increase the surface area. If the original cube were divided into cubes with edges 1 millimeter long, there would be one thousand cubes and they would have a total area of 60 square centimeters. If it were divided into cubes with sides 1 μ (0.001 millimeter) long, there would be a total area of 6 square meters, while if the original cube were divided into cubes with edges 0.001 μ long, the total surface would be 6000 square meters.

Hydration of protoplasm. The particles of many colloids have the property of absorbing and holding large quantities of water. This property is known as hydration, and a colloid which has absorbed water is said to be hydrated. Gelatin is a colloid and affords a good example. A 2 per cent solution of gelatin is a solid at ordinary temperature. Thus two parts of gelatin can hold ninety-eight parts of water. The colloids of protoplasm are hydrated, the degree of hydration varying under different conditions.

Distribution of protoplasm. The protoplasm is usually divided into two parts: the nucleus, a rounded body; and the cytoplasm, which is the protoplasm outside of the nucleus. These are shown in the cells in Fig. 11. Young cells are usually filled with protoplasm. In mature cells the cytoplasm may consist of a layer around the cell walls, a layer around the nucleus, and strands radiating from around the nucleus toward the cell walls (see Figs. 10, 11); or the cytoplasm may simply occur as a layer around the cell walls and the nucleus be embedded in this layer (Fig. 13). The nucleus is generally regarded as the part of the cell which governs the activities of the other parts and determines the nature and hereditary characteristics of the plant. The nucleus is a permanent organ of the cell. Nuclei are produced by the division of one nucleus to form two daughter nuclei. The division of the entire protoplasm (protoplast) of the cell to form two new cells is preceded by the division of the nucleus. The nucleus has a complicated structure and an intricate method of division. The nucleus and its division will be treated much more fully in a later chapter.

Inclusions within the protoplasm. Protoplasm consists essentially of a colloidal dispersion of proteins in water, but many other substances may be found within the protoplasm; these include mineral salts, sugar in solution, and food particles.

Physiological properties of protoplasm. Protoplasm is frequently said to be distinguished from non-living matter by the following physiological properties:

1. *Absorption and excretion.* By absorption protoplasm obtains materials necessary for its growth, and by excretion it gets rid of some substances which it does not need. The protoplasm of green plants takes in water and mineral matter from the soil, and carbon dioxide from the air. In the process of photosynthesis, sugar is manufactured from the carbon dioxide and some of the water. This sugar may be stored in the cells or changed into some other form of stored food; or it may combine with elements from the soil and be stored as food; or it may become incorporated in the protoplasm. Substances which are very different from protoplasm are thus taken into the protoplasm and then combined and made into protoplasm.

2. *Metabolism.* The sum of the processes of chemical change, including the building up and oxidation of material within the protoplasm, is known as metabolism. One of the activities of protoplasm is the combining of sugar with elements from the soil to produce proteins which become a part of the protoplasm. This is a constructive process. Destructive processes also take place in the cells of plants as complex compounds are broken down with the liberation of energy. The protoplasm uses this energy in various activities.

3. *Growth and reproduction.* The growth of protoplasm is due to changes within the protoplasm, while the growth of non-living things, such as ordinary crystals, is accomplished by the addition of layers on the outside. Reproduction is essentially the separation and growth of small portions of protoplasm derived from one or two parent organisms. Reproduction, therefore, is a form of growth.

4. *Movement.* Protoplasm has the power of moving and is frequently in motion. This motion of the protoplasm in a cell can be easily seen with the aid of a microscope. In some cases the motion is evident as an active streaming, while in others it manifests itself by changes in the shape and position of the protoplasmic masses. Fig. 12 shows three drawings, made at fifteen-minute intervals, of the same cell. The changes in the arrangement of the protoplasm are very evident. Protoplasm not only possesses the property of moving but it may also cause the motion of whole organs or even organisms. This kind of movement is more evident in the case of animals than in plants, but is easily recognized in the case of sensitive plants and in leaves which fold together at night. We know also that the younger parts of many plants bend toward the light. Numerous small plants which live in water have the power of moving from place to place, just as is the case with animals.

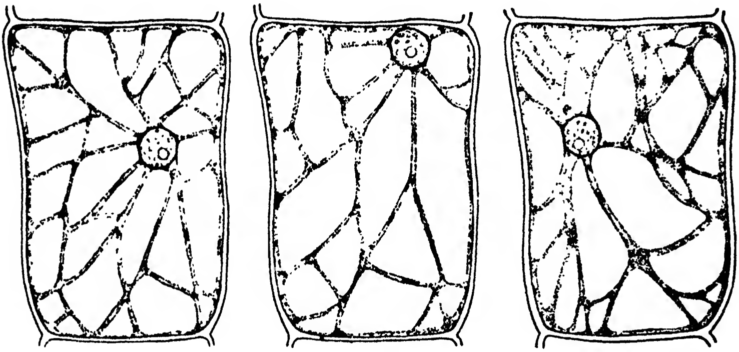

Fig. 12. Drawings, made at fifteen-minute intervals, of a cell from a hair of a squash plant

Note the changes in the arrangement of the protoplasm. (× 180)

5. *Irritability.* The property of responding to external stimuli is known as irritability. A good example is afforded by the effect of various stimuli, such as heat or chemicals, on the movement of protoplasm. Moderate heat increases the rate, while low temperatures decrease it. Some chemicals accelerate it, while others have the opposite effect. The effect of a stimulus on protoplasm

may be evident in the movement of a whole organ, as when the leaves of a sensitive plant close as the result of contact or of heat, or when a stem or a leaf bends toward the light.

Vacuoles. The larger part of the space within a mature cell is usually occupied by a vacuole. This is a clear space which contains water with small quantities of material dissolved in it. The principal use of vacuoles is, by enlarging the cell, to increase its absorbing surface; besides this, water, food, or waste material can be stored in them. Vacuoles are not present in very young cells, but as the cell increases in size small vacuoles appear and then gradually enlarge. As they increase in size they coalesce to form a single large vacuole, the volume of which is usually greater than that of the protoplasm. In a large cell the protoplasm occurs as a layer lining the cell wall, while in addition there may be strands stretching across the vacuole. Fig. 13 shows a young cell without vacuoles, and stages in the formation and growth of the vacuole.

Plastids. These are definitely shaped protein bodies embedded in the cytoplasm. There are several kinds of plastids, and they have different functions. Colorless plastids are known as leucoplasts. Leucoplasts are often juvenile stages of other types of plastids. Amyloplasts are white plastids in which starch is stored (Fig. 51). Colored plastids are known as chromoplasts. In higher plants the most numerous and important of the chromoplasts are the chloroplasts, which are green bodies that are colored by chlorophyll. The small black dots in Figs. 10, 19, and the oval structures in the cells in Figs. 17, 18, are chloroplasts. In the presence of sunlight, carbon dioxide and water in the chloroplasts are changed into sugar. There are various other types of chromoplasts. The red color of tomatoes and the yellow color of the petals of *Tropaeolum* (nasturtium) are due to chromoplasts. Not all colors of flowers and fruits are due to chromoplasts, as such colors are frequently due to pigments dissolved in the vacuoles. Often there is no very sharp distinction between the various types of plastids. Thus, a leucoplast when exposed to the light may develop chlorophyll and become a chloroplast, while in the tomato the chloroplasts develop red pigment as the fruit ripens.

Plastids grow and divide. Chloroplasts can be traced throughout the life cycle of some of the lower plants. In flowering plants the various types of plastids go through stages in which they are very small and colorless, and it is uncertain whether they persist

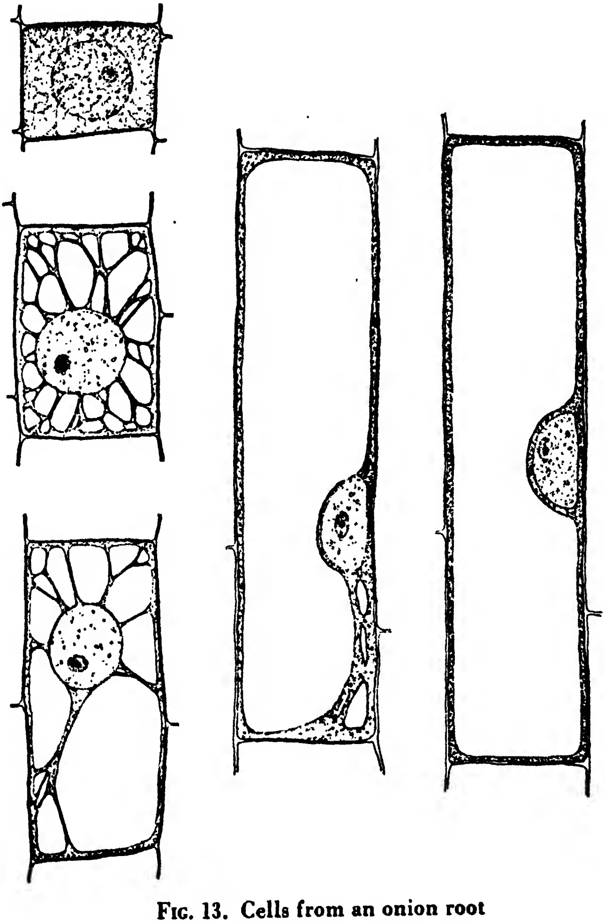

Fig. 13. Cells from an onion root

The cell in the upper left-hand corner is a young one without vacuoles, while the others show various stages in the formation and enlargement of the vacuole. (× 800)

throughout the stages of sexual reproduction or are formed *de novo* in the cells of the developing embryo.

The units of living matter. The cell is the smallest unit of living matter capable of continued independent life and growth, but examination of a cell has shown that it is composed of a number of different small units, all of which combine to carry on the varied activities of the cell. In later chapters we shall have occasion to study the structure of the small units which we have observed in the cell, and we shall find that some of them are in turn very complex and composed of different kinds of smaller units. Therefore, while the cell is the smallest unit of living matter capable of continued independent existence, it is itself a very complex structure composed of many varied smaller units.

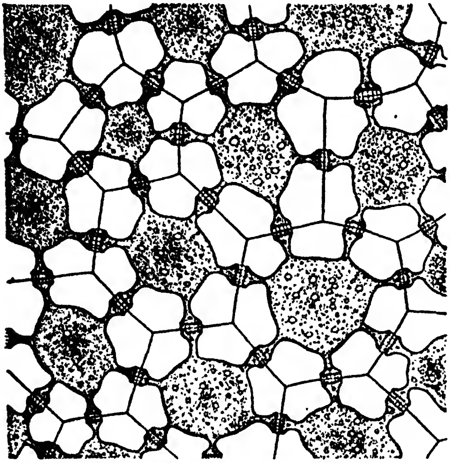

Fig. 14. Cells from the kernel of a fruit of a nipa palm (*Nipa fruticans*), showing protoplasmic connections between adjacent cells

The white areas represent thick cell walls

In at least many cases the cells of higher plants are not absolutely independent, as the protoplasm of neighboring cells is connected by means of fine protoplasmic strands which run through perforations in the cell walls. When the walls are thin it is rather difficult to demonstrate these connections, but they are much more easily seen when the walls are thick. Such connecting strands are shown in Figs. 14 and 54.

CHAPTER IV

THE LEAF

A *leaf* is a lateral outgrowth from a stem and is, typically, a thin, expanded structure with usually a green color (Fig. 15).

While a number of important physiological processes take place in leaves, their principal function, and the one for which their structure is especially suited, is *photosynthesis*. This is the production of sugar from carbon dioxide and water in the presence of sunlight. This process takes place only where there is *chlorophyll*, which occurs in the chloroplasts. The sugar formed in photosynthesis is the basis from which all the complex compounds found in plants are produced. The thin, expanded form of leaves is especially suited for photosynthesis, as light, which is necessary for this process, penetrates only a short distance into a plant. An increase in the thickness of leaves would require additional plant material without producing a corresponding increase in the rate of photosynthesis.

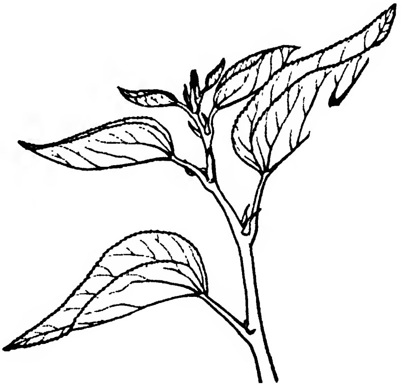

FIG. 15. Young leaves of mulberry (*Morus alba*)

Stipules occur at the bases of all except the oldest; here there is a scar showing where the stipule was located. (×⅓)

Structure of leaves. Leaves (Fig. 15) are typically composed of a broad, expanded portion, the *blade*, which is the essential part; a stalk, called the *petiole*, which is sometimes lacking; the *base*, the part which joins the leaf to the stem; and often a pair of *stipules*, which are scalelike or, rarely, leaflike outgrowths from the base. Frequently the stipules are temporary structures and drop off as the leaf matures (Fig. 15).

Leaves are distinguished from stems by their origin, the leaf being the first lateral outgrowth from the stem (Fig. 113), while the branches grow in the axils of the leaves, that is, just above where the leaves are joined to the stem. Leaves are further distinguished from stems by the fact that the growth of a leaf is usually limited, while that of most stems is not; that is, leaves reach a certain size and then cease to grow, while stems continue to grow in length as long as the plant lives.

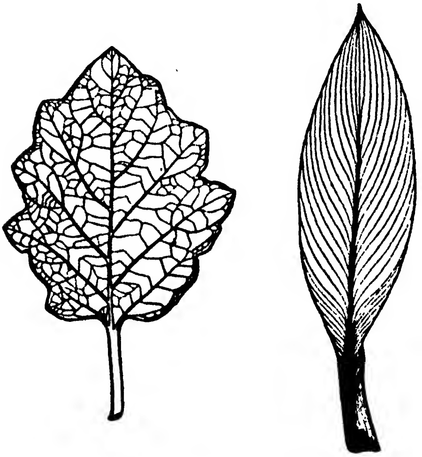

Fig. 16. Venation of leaves

Left, leaf of eggplant, showing midrib and netted veins; right, canna leaf with parallel veins

The blades of most leaves contain a narrow thickened structure which is a continuation of the petiole and extends from the petiole through the center of the blade to the opposite end (Fig. 16). This is the *midrib*. On both sides of the midrib there are lines which either are parallel with each other or form a network. These are *veins*. The midrib and veins contain conducting cells, through which water, coming from the roots, is carried to all parts of the leaf, and food, manufactured in the leaf, is conducted to the petiole on its way to other parts of the plant. The midrib and veins are also important in giving stiffness to the leaves. Some leaves do not have a single midrib but have several large veins which serve the same purpose (Figs. 34, 38).

Venation. The leaves of flowering plants show two very distinct types of *venation*, that is, arrangement of the veins. In one type the veins are *parallel* (Fig. 16); in the other they form a network (Fig. 16), and are said to be *netted*. These two types of venation are characteristic of the two great divisions of flowering plants, monocotyledons and dicotyledons. *Monocotyledons* are plants with

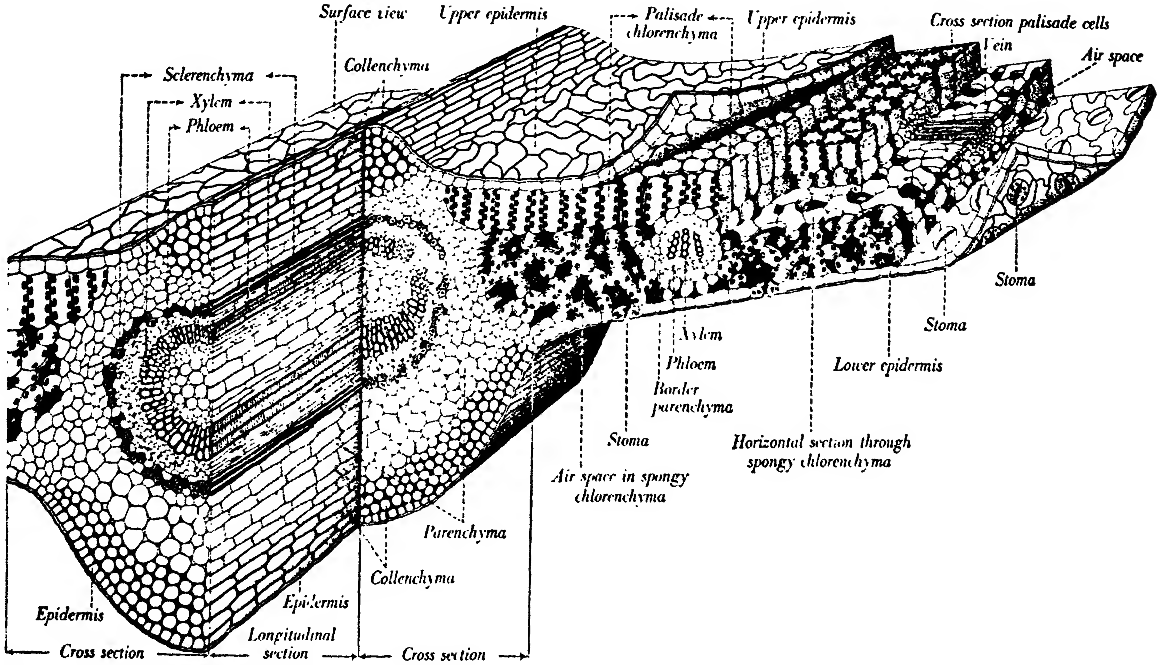

Fig. 17. A section of a midrib and a small part of the leaf blade dissected to show the arrangement of the tissues

On the left is a cross section of half of the midrib followed by a longitudinal section, and this by a cross section of the remainder of the midrib and a portion of the blade. The leaf blade on the right is dissected in various ways one seed leaf, *dicotyledons* have two seed leaves. Parallel veins are characteristic of monocotyledons, and netted veins of dicotyledons, although some monocotyledonous leaves have netted veins.

MICROSCOPIC ANATOMY OF LEAVES

A leaf is composed of various groups of cells which are known as tissues. The different tissues are characterized by different types of structures and are fitted for different functions. In Fig. 17 is a section of a leaf dissected to show the different tissues and their arrangement in the leaf. In the following paragraphs the different tissues will be described and illustrated. Referring to Fig. 17 will make their relation to each other clearer.

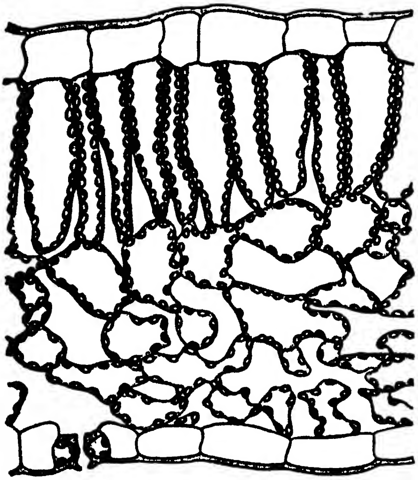

FIG. 18. Cross section of a portion of the blade of a leaf. (× 285)

Epidermis. The leaf is covered on both surfaces by a single layer of cells, known as the *epidermis* (Fig. 18). The outer walls of the epidermis are usually thickened and impregnated with a waxy substance called *cutin*. Walls that are impregnated with cutin are said to be *cutinized*. Not only do the outer walls of the epidermis contain cutin, but their outer surfaces are frequently covered by a layer of cutin which is known as a *cuticle*. Water passes readily through cellulose, and so, if the outer walls of the epidermis were thin cellulose walls, their outer surfaces would be wet and water would evaporate from them in large quantities. The evaporation of water from plants is called *transpiration*. As the outer walls of the epidermis are thick and waxy, water does not pass through them readily, and the transpiration of water from the surface of the epidermal cells is greatly reduced, only very small quantities of water being lost in this manner. This restriction of transpiration is one of the most important functions of the epidermis. Another function is the prevention of the entrance of disease-producing organisms into the interior of the leaf. The epidermis also protects the soft interior from mechanical injury.

In the epidermis of the leaf are numerous small openings, the *stomata*. These are shown in Fig. 19, as seen in the surface of the epidermis. The small oval openings are the stomata; the large, irregularly shaped cells are ordinary epidermal cells. A cross section of a stoma is shown in Fig. 18, in the lower epidermis.

Each stoma is surrounded by two kidney-shaped cells called *guard cells*. Under certain conditions these guard cells move in such a way as to open or close the stomata. The stomata allow for the exchange of oxygen and carbon dioxide between the cells in the interior of the leaf and the external atmosphere, and also permit the passage of water vapor from the interior of the leaf to the outside air.

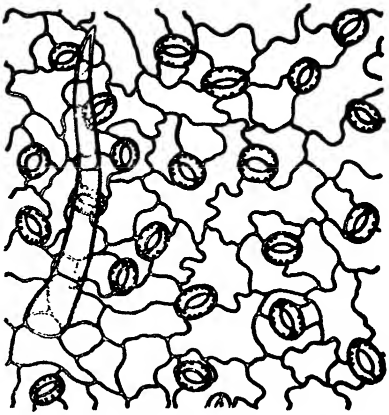

Fig. 19. Surface view of epidermis of a dicotyledonous leaf

The oval openings are the stomata. Each is surrounded by two kidney-shaped guard cells containing chloroplasts. The large irregular cells are ordinary epidermal cells. An epidermal hair is shown at the left. (× 150)

Distribution of stomata. Stomata are usually found only in the lower epidermis, or much more abundantly in the lower than in the upper epidermis. This would seem to be explained in part by the fact that stomata in the lower surface are less likely to be closed by rain or by dust than are those in the upper epidermis. In leaves which float on the surface of the water stomata occur only in the upper epidermis. Submerged plants have no stomata.

Chlorenchyma. The parts of the leaf that lie within the epidermis and between the veins are especially suited to carrying on photosynthesis. The cells in this part of the leaf contain chloroplasts, and are known as *chlorenchyma* cells (Fig. 18).

Palisade chlorenchyma. The chlorenchyma is usually divided into two regions. The portion near the upper surface is generally composed of elongated cells which are close together, with their longest axis perpendicular to the epidermis (Figs. 18, 30, 48). When we look at a section of a leaf, these cells have an appearance resembling a palisade. They are called palisade cells or *palisade chlorenchyma.* The palisade chlorenchyma may consist of a single layer of cells or of two or more layers. These cells, being near the upper surface of the leaf, are in a favorable position to receive sunlight, and their chief function is to carry on photosynthesis. Their elongated shape is favorable to this function, as the light in going through them does not pass through many cell walls. Between the palisade cells are small air spaces which are connected with larger spaces in the lower part of the leaf, and through these with the stomata in the lower epidermis. These air spaces make it possible for gases to diffuse to and from the palisade cells. In Fig. 20 is shown a section cut across the palisade layer in a plane perpendicular to the longest axis of the cells and parallel with the epidermis. This section shows very plainly the air spaces which extend up between the palisade cells.

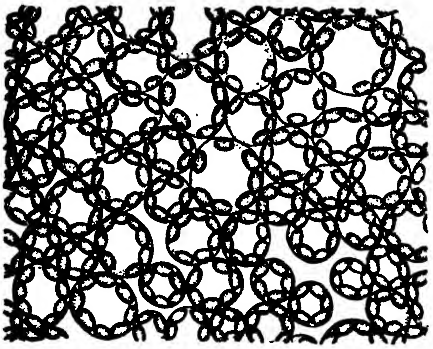

Fig. 20. Section of palisade of a leaf, cut parallel with the epidermis. (× 425)

The cells of the chlorenchyma contain a large central vacuole and a thin layer of protoplasm lining the wall. The chloroplasts are embedded in this protoplasm and are close to the cell wall.

Spongy chlorenchyma. The lower portion of the chlorenchyma is known as *spongy chlorenchyma* and is usually composed of cells more irregular in shape and arrangement than the palisade cells (Figs. 18, 21, 30). Also, this region generally contains large air spaces. The cells of the spongy chlorenchyma contain chloroplasts and carry on photosynthesis, but they are not in as favorable a position for receiving light as are the palisade cells, and they have fewer chloroplasts. They are not, therefore, so important from the standpoint of photosynthesis as are the palisade cells. On the other hand, the large air spaces that surround these cells are near the stomata and directly connected with them (Fig. 18). There is therefore a much freer circulation of gases around these cells than around the palisade cells, with the result that they are better suited to the exchange of gases between the cells and the surrounding atmosphere. The air spaces of the spongy chlorenchyma are not isolated chambers but a series of intercommunicating passages. While it is customary to speak of the air spaces in the spongy chlorenchyma as though there were many of them, it would be just as correct to consider many of them as forming a single large air space in which, in the case of the spongy chlorenchyma, the cells are loosely arranged. A good idea of the shape of these passages can be obtained by reference to Fig. 17 and by comparing Fig. 18 with Fig. 21, which represents a section through the spongy chlorenchyma parallel with the epidermis.

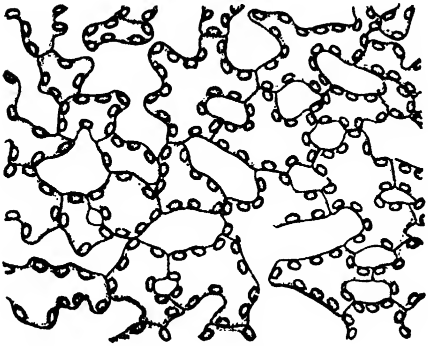

FIG. 21. Section, cut parallel with the epidermis, through the spongy chlorenchyma of a leaf. (× 425)

Owing to the fact that the chloroplasts are closer together in the palisade chlorenchyma than in the spongy chlorenchyma, the upper surfaces of many leaves appear to be deeper green than the lower surfaces.

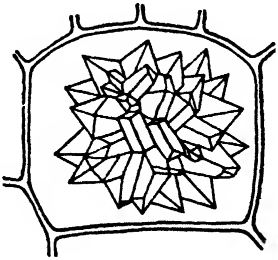

FIG. 22. Rosette crystal from cell in a leaf. (× 730)

Calcium oxalate crystals. The leaves and other organs of many plants contain conspicuous crystals of calcium oxalate, which appears to be a waste product. The forms of the crystals are very diverse. One of the commonest is a compound crystal having the appearance of a rosette and known as a *rosette crystal* (Fig. 22). Another common form is a long, slender crystal, or *raphide*. Such crystals usually lie parallel to each other in a bundle, which is sometimes found in a special saclike cell (Fig. 23). In certain cases these cells have tapering end walls which are thin at the apices (Fig. 23); when the sacs are injured mechanically, the raphides are shot through the thin points (Fig. 24). Certain kinds of raphides are very irritating and seem to afford some protection from animals, although many plants with raphides are eaten by animals. At least in some cases, the pain produced is due to the entrance of an irritating substance into the wound rather than to the raphides themselves. Raphides are destroyed by boiling, and so food plants containing them are not irritating when cooked.

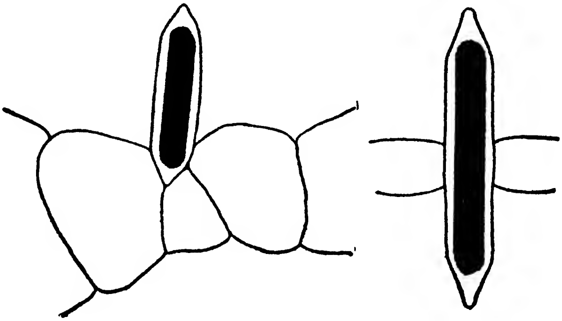

FIG. 23. Raphides from leaves

Left, taro (*Colocasia esculenta*); right, *Pistia stratiotes*. (× 160)

Calcium carbonate (limestone) is much less abundant in plants than calcium oxalate. It is, however, deposited in some plants in the form of cystoliths (Fig. 25). The main body of a cystolith is a cellulose extension of the cell wall in which the calcium carbonate is deposited in the form of fine granules.

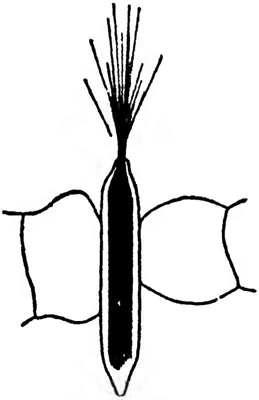

FIG. 24. Ejection of raphides from saclike cell of *Colocasia esculenta*. (× 160)

The midrib. The functions of the midrib are to strengthen the leaf; to convey food, manufactured in the leaf, toward the petiole; and to carry water from the petiole to various parts of the blade. The midrib is composed of the tissues described in the following paragraphs. A *tissue* is a group of contiguous cells having the same general characteristics. Cross sections of midribs are shown in Figs. 26 and 28.

Collenchyma. There are two ways in which cells give strength to plant organs. In some cases the cell walls are very greatly thickened, and the thickened cell walls give strength. This is true of the wood of woody stems. Other cells become stretched by the water which is in them, and therefore are rigid. Such cells may serve to strengthen organs. Cells which are stretched by the water in them are said to be *turgid*. The rigidity derived from turgidity has some points of similarity to that of a hose full of water, or that of an automobile tire filled with air under pressure.

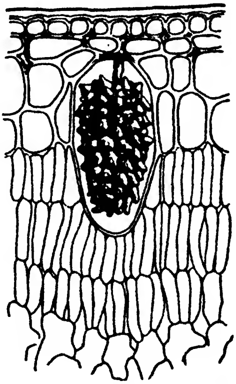
FIG. 25. Cystolith in leaf of India rubber tree, *Ficus elastica*. (After Sachs)

In the center of the upper portion of the midrib, just below the epidermis, there is usually a group of cells which give strength both by having thickened walls and by being turgid. A group of the same kind of cells usually occurs also just above the lower epidermis. These cells are known as collencnyma. In Fig. 26 the collenchyma is shown as a crescent-shaped layer around the lower part of the midrib and just within the epidermis; also as a small group of cells extending into the projection from the upper surface of the midrib. In the section shown in Fig. 28 the collenchyma is in the same position as in Fig. 26, but is less evident because the walls are not greatly thickened. Collenchyma is composed of living cells with walls which are thickened at the angles where three or more cells come in contact with one another. This is clearly shown in Fig. 27. The thick places in the walls increase the strength of the cells, while the thin places allow for a more rapid transfer of materials from cell to cell than would take

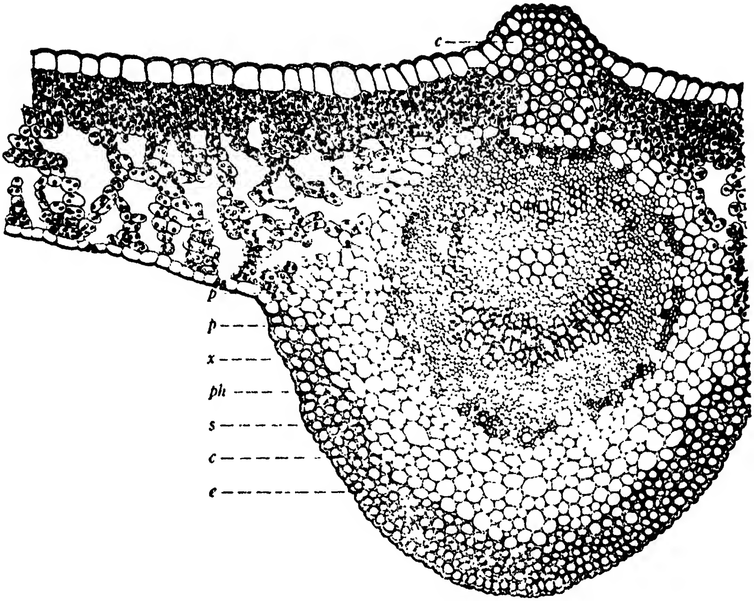

Fig. 26. Cross section of a midrib of a leaf (*Ixora*)

On the left is a portion of the thin part of the blade, showing upper and lower epidermis and chlorenchyma. *e*, epidermis; *c*, collenchyma; *p*, parenchyma; *s*, sclerenchyma; *ph*, phloem; *x*, xylem. (× 185)

place if the cell walls were thickened throughout. These cells are more or less turgid, and so give strength to the leaf in this way also.

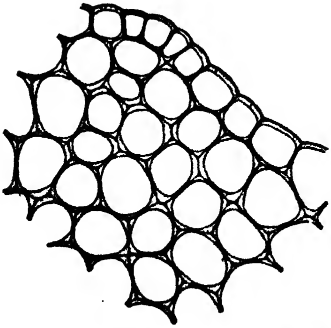

Fig. 27. Cross section through the epidermis and collenchyma of a *Coleus* stem. (× 245)

The weight of the leaf causes it to tend to bend downward, with the result that there is a tendency for the upper portion to be stretched and the lower portion compressed. The collenchyma occurs, therefore, in those parts of the midrib in which there is the greatest need for strengthening material.

Parenchyma. The regions between the collenchyma cells and the central portion of the midrib are occupied by *parenchyma* cells.

In Fig. 26 this parenchyma is shown as a ring of tissue which in the drawing appears to be lighter-colored than any of the tissues touching it. This lighter appearance is due to the combination of the large size of the cells, the thin walls, and the absence of chloroplasts. In structure the parenchyma cells are not specially modi-

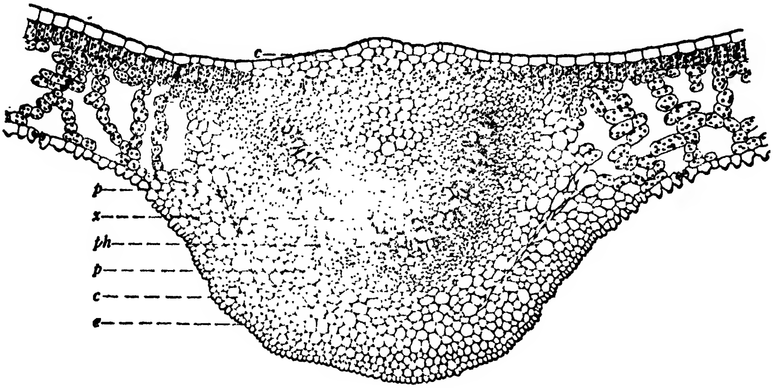

Fig. 28. Cross section of a midrib and adjoining portion of thin part of the blade of coca leaf (*Erythroxylon coca*)

e, epidermis; *c*, collenchyma; *p*, parenchyma; *ph*, phloem; *x*, xylem. (× 66)

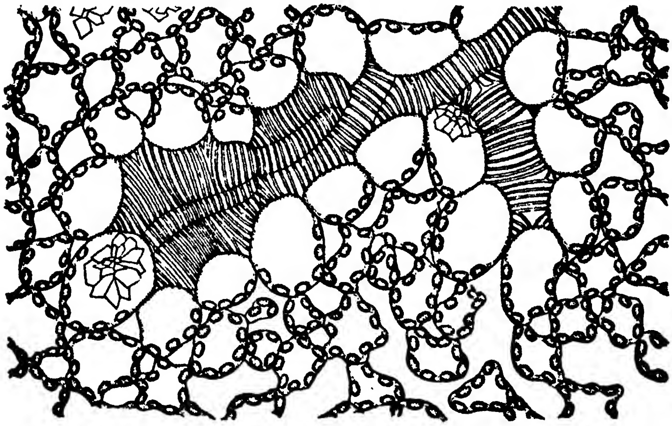

Fig. 29. Termination of veins in a leaf, as seen in a section cut parallel with the epidermis. (× 425)

fied for any particular function, but they perform all the general functions of cells to a limited extent. Parenchyma cells have thin walls, but on account of their turgidity they strengthen the midrib. That a considerable part of the stiffness of most leaves is due to the water in their cells can be readily demonstrated by means of leaves which have been severed from a plant. Such leaves continue to lose water by transpiration. As this water is not replaced, the cells of the leaf will contain less and less water and will lose their turgidity. We see the result when the leaf wilts and becomes soft.

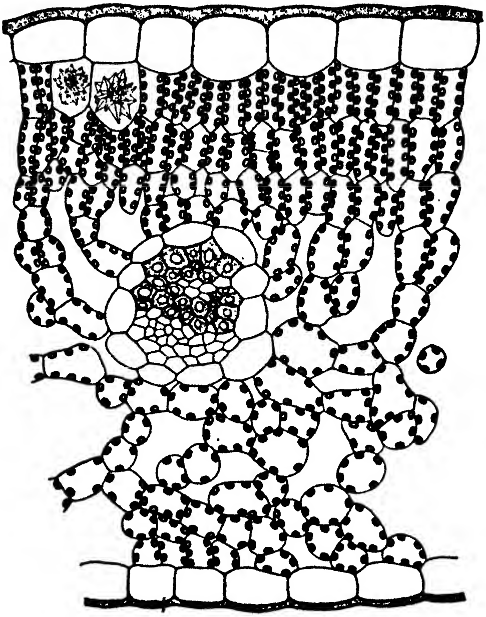

FIG. 30. Cross section of the thin part of a leaf (*Ixora*), showing the connection of the chlorenchyma with a vein

The vein is seen in the center as a compact group of cells. (× 215)

Conducting system. The tissues composing the conducting system are situated near or at the center of the midrib. This system, as seen in cross section, usually has the form of a ring (Fig. 26), a crescent-shaped ring, a crescent (Fig. 28), or scattered patches, but may have other shapes. If it is in the form of a ring, parenchyma cells are usually found within the ring (Fig. 26). The inner part of the ring is composed of *xylem*, which is conspicuous on account of its having thick-walled cells. Xylem conducts water and, on account of its thick-walled cells, gives strength. The conducting elements of the xylem are long tubes composed of dead cells.

The xylem ring is surrounded by a ring of *phloem*, which is composed of thin-walled cells (Fig. 26) and serves for the transportation of food materials that come from the chlorenchyma of the leaf. When the xylem, instead of being in the form of a ring or a crescent-shaped ring, has the form of a crescent, the phloem may occur only below the xylem (Fig. 28) or may be both above and below it.

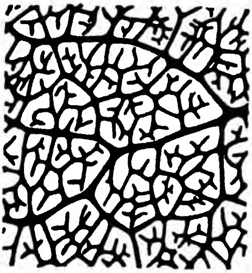

Fig. 31. Arrangement of netted veins and the free ends of the veinlets in a small portion of a leaf of a lime (*Citrus aurantifolia*). (× 6)

The conducting system is better developed in the stem than in the leaf and will be considered in greater detail in the chapter dealing with the stem.

Sclerenchyma. Thick-walled dead cells are frequently found scattered in the parenchyma just outside of the phloem (Fig. 26). These are strengthening cells and are known as *sclerenchyma.* They are greatly elongated in the longitudinal direction of the midrib. Their position just exterior to the thin-walled phloem affords mechanical protection to the latter.

Veins. The structure of large veins is similar to that of a midrib. The complexity of the structure decreases with the size of the veins until, near their ends, small veins consist of only one or a few conducting cells (Fig. 29). The cells of the chlorenchyma are usually arranged so that the conduction of materials to and from the veins is facilitated (Fig. 30). In Fig. 31 are shown the arrangement of the netted veins and the free ends of the veinlets in a small portion of a dicotyledonous leaf.

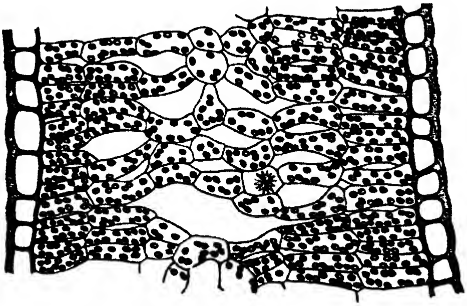

Fig. 32. Section of a vertical leaf of *Eucalyptus*, showing a palisade layer on each side. (× 275)

Vertical leaves. The leaves of many species of *Eucalyptus* do not spread out horizontally but hang vertically, so that both surfaces of the leaf receive direct sunlight. In keeping with this fact, palisade chlorenchyma is developed on both sides, as shown in Fig. 32.

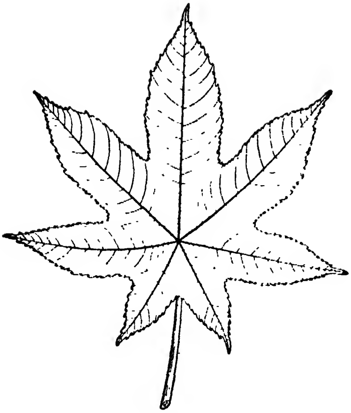

FIG. 34. Peltate leaf of castor-oil plant (*Ricinus communis*). (× ¼)

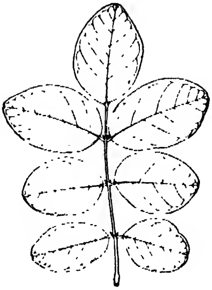

FIG. 35. Pinnate leaf (*Clitoria ternatea*). (× ⅓)

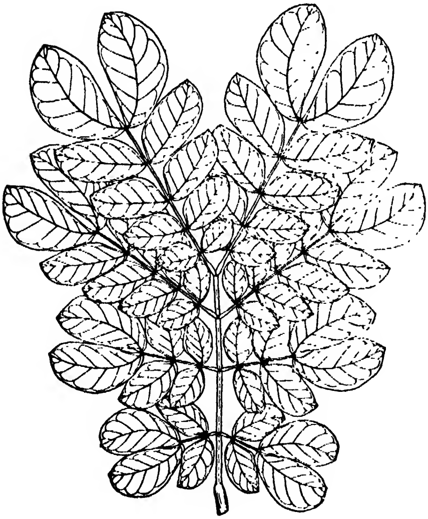

FIG. 36. Bipinnate leaf of rain tree (*Enterolobium saman*). (× ¼)

See Fig. 125

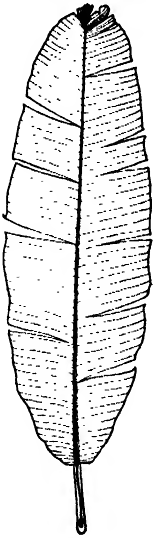

FIG. 37. Leaf blade of banana. (× 1/17)

strengthening tissue to protect them from being torn. The huge entire blades of the banana (Fig. 37) show an interesting modification in that they are not greatly strengthened but instead have certain weak structural lines where the leaf can be torn by the wind without any particular damage to the plant.

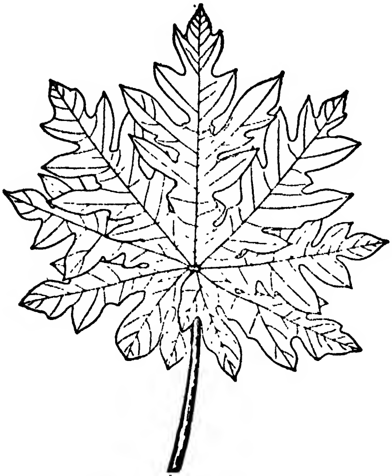

FIG. 38. Lobed leaf of papaya (*Carica papaya*). (× ⅛)

The papaya is a small herbaceous tropical tree with melonlike fruits. They are among the most popular and widely used of tropical fruits. (See Fig. 293)

Plants having unbranched stems must have large leaves if they are to expose an extensive surface to the light. In keeping with this fact we find that large palms and tree ferns have enormous leaves. On the other hand, plants with many small branches have small leaves.

The general shape of leaves is related to their arrangement on the stem. When leaves are densely crowded they are usually *linear* (long and narrow), and so shade each other much less than would broad leaves. When less crowded the leaves are more often somewhat oval in outline, and when still less crowded they are apt to approach a circular shape.

When leaves are lobed, the lobing follows the large veins (Fig. 38), so that the photosynthetic tissue is nearer the principal veins than would be the case if the leaves were entire.

TRICHOMES

Some of the epidermal cells of most plants grow out, singly or less frequently in groups, to form appendages which are known as *trichomes* or hairs. Frequently the trichomes lose their protoplasmic contents and become filled with air. The young leaves of many plants have trichomes which are shed as the leaf becomes older. Cotton consists of long unicellular hairs which grow from the epidermis of cotton seeds.

Trichomes exhibit a great variety of form and vary from small protuberances of the epidermal cells to complex branched multicellular structures (Figs. 39, 40). Even the simple unbranched hairs show great variety. Such trichomes may be unicellular or multicellular; they may be straight or curly, project straight from the epidermis or lie parallel with it. When they lie against the surface of the leaf and all point in the same direction, they produce a silky appearance. The methods of branching exhibited by the trichomes are very diverse. Among the most beautiful forms of trichomes are those known as scales. These are flat structures having short central stalks (Fig. 41). Scales are sometimes found so close together as to form an almost complete covering over the surface of a leaf.

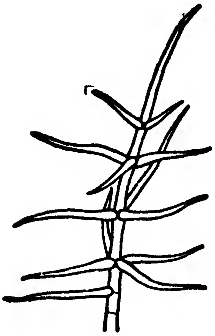

Fig. 39. Branched hair of *Callicarpa caudata.* (× 50)

A dense covering of dead trichomes has a tendency to restrict the rate of transpiration. The transpiration of a leaf in still air brings into being a layer of moist air around the leaf, and the diffusion of water from the leaf into this moist air is less rapid than the diffusion of water into dry air would be. When there is free movement of air around the leaf, wind will replace the moist air with drier air. A dense layer of trichomes tends to reduce the movement of the air and so to lower the rate of transpiration. A great development of trichomes may also, by producing a screen, reduce the heating effect of sunlight. Hairs are usually most numerous on the under, or stomata-bearing, surface of the leaf. While a dense covering of trichomes retards transpiration, the hairs of many leaves appear to be too scattered to have any appreciable effect.

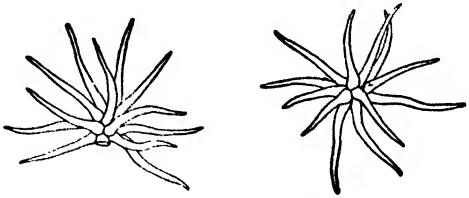

Fig. 40. Side and top views of stellate hair of *Callicarpa erioclona.* (× 350)

A covering of hairs, by holding a layer of air near the leaf, may prevent water from reaching and clogging the stomata. When a leaf with such a coating of trichomes is submerged in water, the layer of air near the epidermis glistens with a silvery sheen. Although submerged, the epidermis may remain dry for a considerable length of time. Even such short trichomes as those that are shown in Fig. 48 may be very effective in keeping water from the stomata. While trichomes may restrict the rate of transpiration, they not only do not interfere with the diffusion of carbon dioxide into the leaf but may actually assist in keeping open a passageway for this diffusion when the stomata might be clogged as the result of rain or dew.

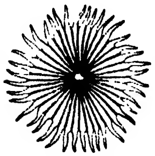

Fig. 41. Scale of *Elaeagnus philippensis.* (× 75)

Bristlelike hairs. A number of plants possess stiff, sharp-pointed, bristlelike hairs which readily penetrate the skin of man and produce very disagreeable effects. Some of the hairs of this type have barblike protuberances along their sides (Fig. 42); these protuberances increase the irritating effect of the trichomes. Bristlelike hairs may afford protection to plants by preventing animals from eating the leaves, but comparatively few plants have hairs stiff enough to be very effective in this way.

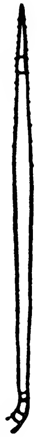

Fig. 42. Bristlelike hair of cowitch (*Mucuna pruriens*). (× 30)

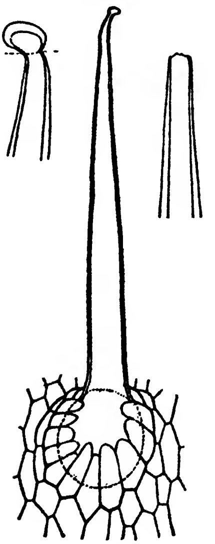

Fig. 43. Stinging hair of a nettle (*Laportea meyeniana*). (Central drawing × 150)

Stinging hairs. Stinging hairs (Fig. 43) are one of the most interesting types of trichomes. A typical stinging hair contains a poisonous liquid and consists of a basal bulb-shaped portion from which projects a stiff, slender, tapering structure that ends in a small knob or a sharp point. Near the tip there is usually an oblique thin place in the wall, so that when the body of an animal or some other object is pressed against the tip with sufficient force, the tip is broken off, leaving a sharp point that can readily penetrate an animal's skin. The wall of the rounded basal portion is distended by the pressure of the contained liquid, and it contracts when this pressure is removed by the breaking of the tip. This contraction tends to force the fluid through the opening in the tip, so that an animal into which the sharp point has stuck will be injected with the poisonous fluid. The pressure of the animal against the hair also helps to force the liquid from the bulbous base.

Glandular hairs. A great variety of plants have glandular hairs (Fig. 44). These secrete oil, resin, or mucilage. A typical glandular hair consists of a stalk and an enlarged terminal portion, which is the gland proper. This may be unicellular or multicellular. The strong odors of many plants are due to the excretions of glandular hairs.

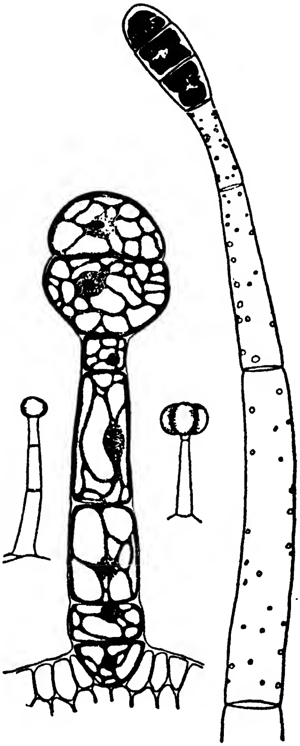

Fig. 44. Glandular hairs

Left, water hyacinth; second figure, squash; third figure, tomato; right, tobacco. (× 200)

CHAPTER V

ASSIMILATION AND USE OF MATERIALS

Assimilation includes processes by which an organism changes nutritive materials to the kind of substances of which it is composed, and processes by which these substances are incorporated into its body. Assimilation in one form or another takes place in all parts of a plant. The basic process on which all other assimilation depends is photosynthesis. Photosynthesis is carried on in all green parts of a plant; but the leaves are the organs which are especially fitted for photosynthesis, and so it is convenient to consider assimilation in connection with the leaf.

PHOTOSYNTHESIS

Definition. Photosynthesis is the formation of sugar from carbon dioxide and water in the presence of light; it takes place only where there is chlorophyll, which is found in the chloroplasts.

Source of material. The water used in photosynthesis is absorbed by the plant roots and then carried to the leaves. The carbon dioxide diffuses from the atmosphere through the stomata and then through the intercellular spaces. Carbon dioxide cannot enter the cells as a gas, but water from the cells permeates the cell walls of the chlorenchyma, and the carbon dioxide gas goes into solution in this water. As the water in the walls is continuous with that in the cells, the carbon dioxide in solution in the cell walls diffuses into the cells and finally reaches the chloroplasts.

Diffusion is always from the region of greater concentration to that of less concentration. The using up of carbon dioxide in the chloroplasts creates in the immediate vicinity a region where the concentration of carbon dioxide is low. This causes carbon dioxide to diffuse from the protoplasm and cell walls toward the chloroplasts. In turn, carbon dioxide diffuses from the intercellular spaces and goes into solution in the water in the cell wall. The result is that the concentration of carbon dioxide is less in the intercellular spaces than in the external atmosphere, and so there is a diffusion of carbon dioxide from the external atmosphere through the stomata into the intercellular spaces. The movement of carbon dioxide is, then, from the external atmosphere through the stomata into the intercellular spaces, into solution in the cell walls, then by diffusion into the protoplasm, and finally into the chloroplasts.

Process. Photosynthesis is a very complex process concerning the details of which we have very little actual information. The first stable product seems to be some form of sugar. The various sugars have complex molecules, however, and it would not seem probable that one of them is the first compound formed. Various intermediate compounds are postulated by different theories, but none of these theories is supported by sufficient evidence to warrant its acceptance at the present time. As the result of the photosynthetic process, *glucose* (grape sugar), which has the formula $C_6H_{12}O_6$, accumulates in the leaf, and this is generally regarded as the first stable product.

The theories which have been most widely held are Baeyer's hypothesis and modifications of it. Baeyer assumed that in the plant carbon dioxide was changed to carbon monoxide and oxygen ($CO_2 \longrightarrow CO + O$); and that the water was changed to hydrogen and oxygen ($H_2O \longrightarrow H_2 + O$). The carbon monoxide and hydrogen then united to form formaldehyde ($CO + H_2 \longrightarrow CH_2O$), after which six molecules of the formaldehyde were condensed to form a molecule of glucose ($6\,CH_2O \longrightarrow C_6H_{12}O_6$).

A great objection to this theory has been that formaldehyde is exceedingly poisonous. Attempts have been made to meet this objection by assuming that formaldehyde is never present in anything except in very minute quantities, as it is condensed immediately to form sugar. Also various complicated modifications of Baeyer's hypothesis have been proposed. If Baeyer's hypothesis were true, it would afford a comparatively simple explanation of the chemical changes taking place during photosynthesis. At the present time there are some authorities who maintain that formaldehyde is an intermediate product of photosynthesis, and others who claim that there is no evidence for this view.

If we regard glucose as the end product of photosynthesis, the formula for this process may be written as follows:

$$6\,CO_2 + 6\,H_2O \longrightarrow C_6H_{12}O_6 + 6\,O_2.$$

This formula shows not only that glucose is formed in photosynthesis, but also that oxygen is liberated as a by-product. Moreover, the formula indicates that the number of molecules of oxygen liberated is the same as the number of molecules of carbon dioxide absorbed. This is approximately what has been observed in actual experiments.

The water and carbon dioxide that enter the reaction are very stable compounds, and the liberation of the oxygen requires energy. This energy is supplied by light, which accounts for the necessity of light for photosynthesis. Light by itself does not, however, decompose carbon dioxide or water, so that the plant must have some means of applying the energy of light for this decomposition. The application of the energy of light for the separation of oxygen from carbon dioxide and water appears to be the function of the chlorophyll.

In nature the light used in photosynthesis comes from the sun, but light from other sources can also be used.

Chlorophyll. Chlorophyll is formed in flowering plants only in the presence of sunlight. This explains why the inside of the head of a cabbage is white; it also explains the practice of banking celery in order to blanch it. Chlorophyll is not a single compound but a mixture of pigments including two green ones, chlorophyll A and chlorophyll B, and two brown ones, carotin and xanthophyll. Chlorophyll does not contain iron, but iron is necessary for the formation of chlorophyll.

Products. The two products of photosynthesis are simple sugar and oxygen. The sugar manufactured by plants serves them as food, from which, with the addition of materials from the soil, they elaborate all the complex substances found in them. As photosynthesis is necessary for the manufacture of all the food used by plants, it is indispensable for their existence.

Some of the oxygen liberated in photosynthesis is used by the plants in respiration, but most of it diffuses out of the cells into the intercellular spaces and then through the stomata into the external atmosphere.

When photosynthesis is active, sugar is formed much faster than it is used by the leaf or conveyed to other parts of the plant. Under these conditions much of the sugar in the leaf is transformed into starch, which is insoluble in water at ordinary temperatures. At night, starch is changed back into sugar and is conducted away from the leaf. Starch occurs as small grains which differ in appearance according to species (Fig. 45). The grains of many species show striations as if the material had been deposited in successive layers.

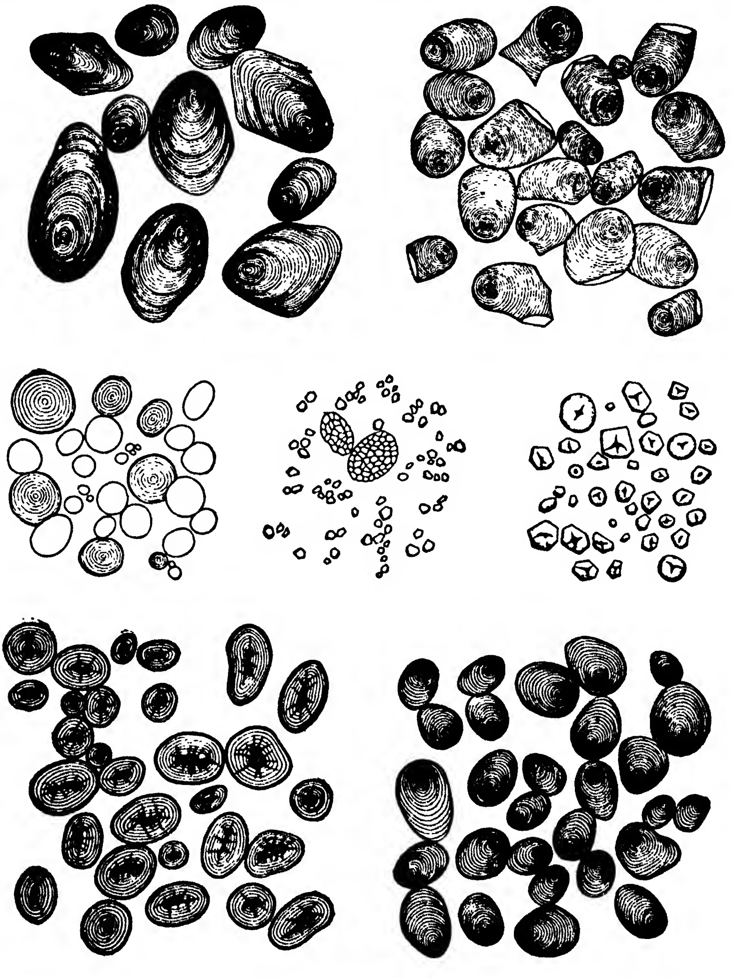

FIG. 45. Starch grains

Upper row, potato and sago; second row, wheat, rice, and corn; third row, bean and *Maranta*. (× 290)

The amount of carbohydrate manufactured by plants varies very greatly with different plants and different conditions, but it has been calculated that as a rough average a plant will manufacture at least one gram of sugar per square meter of leaf surface on a summer day.

Demonstration. Starch is formed in leaves very soon after photosynthesis begins. This is of great advantage in demonstrating the general facts of photosynthesis, as the test for starch is very simple. It consists in treating the material to be tested with a solution of iodine, which gives starch a blue color. In working with leaves the chlorophyll is first extracted, after which the leaves are placed in the iodine solution.

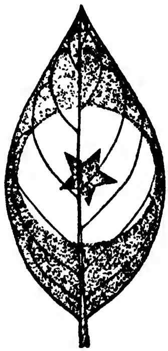

Fig. 46. A leaf tested with iodine for starch after the part showing as a star and that outside of the circle had been exposed to the light and the remainder kept in the dark

The necessity of light for photosynthesis can be shown by keeping a leaf or a part of a leaf in the dark (being careful that all parts of the leaf have a plentiful supply of air) and then testing for starch. The leaf or the part of the leaf which was in the dark will remain white, while that which was in the light will turn blue (Fig. 46).

The necessity for chlorophyll is shown by the fact that starch is not formed in those parts of variegated leaves which lack chlorophyll.

Leaves will not produce starch in an atmosphere that lacks carbon dioxide. If a plant is placed in an atmosphere containing a known quantity of carbon dioxide, it will be found that carbon dioxide is absorbed and that the carbon appears in the leaf in the carbohydrates formed as a result of photosynthesis.

That water is used in photosynthesis is shown by the fact that the carbohydrates produced by this process contain hydrogen, which must have been derived from water.

That oxygen is given off in photosynthesis can be shown very simply by the use of certain water plants which during photosynthesis give off bubbles of gas. This can be collected by the arrangement shown in Fig. 47. If a glowing splinter is inserted into the gas, the brightness of the glow is greatly increased, thus indicating a high percentage of oxygen.

Relation to animals. Photosynthesis is the source of all the food of animals. Animals do not possess the power of manufacturing food from simple inorganic compounds, but must obtain food that has already been elaborated.

In respiration, animals take up oxygen and give off carbon dioxide, so that if there were no plants to separate oxygen from carbon dioxide, the supply of oxygen would be used up and animals cease to exist.

From what has been said it will be seen that, indirectly, photosynthesis furnishes man with the food he eats and the oxygen he breathes, and that it is also the source of his clothing and such of his other necessities as come from plants and animals.

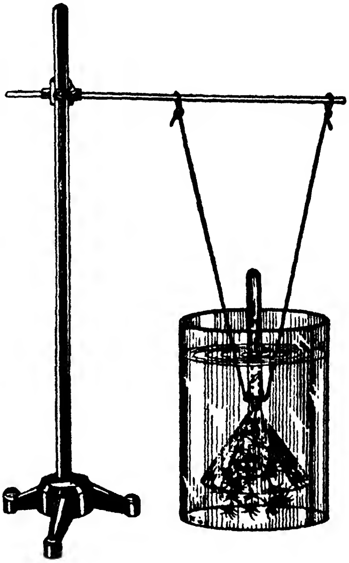

FIG. 47. Apparatus for collecting the bubbles of gas given off by a submerged plant during photosynthesis

Supply of carbon dioxide. The rate of photosynthesis is influenced by various factors, among which are the amount of carbon dioxide present, the intensity of the light, the temperature, and the amount of water present in the plant and in the atmosphere.

The amount of carbon dioxide present in the air is fairly constant, and is about 0.03 per cent of the total gases of the atmosphere. Under natural conditions the rate of photosynthesis is, therefore, not greatly influenced by any change in the concentration of carbon dioxide. However, the rate of photosynthesis can be decreased or increased by artificially decreasing or increasing the amount of carbon dioxide. Growth in greenhouses has been considerably increased by supplying additional carbon dioxide. Doubling the amount of carbon dioxide available about doubles the rate of photosynthesis. When plants are grown in heavily manured beds, part of the increased growth obtained is due to extra carbon dioxide furnished by the decaying material. Under natural conditions the amount of food which a leaf could produce is greatly lessened by the natural deficiency in the supply of carbon dioxide.

Light. As light furnishes the energy for photosynthesis, it would be natural to suppose the rate of photosynthesis would increase with increases in the intensity of light. This is true with low intensities. From very low intensities up to about one-fourth the intensity of full sunlight, there is steady increase in the rate of photosynthesis with each increase in intensity. Under natural conditions, further increases in the intensity of light are nothing like so effective. These further increases produce less and less increase in the rate of photosynthesis. The result observed is probably, to a considerable extent, due to the deficiency in carbon dioxide noted in the last paragraph.

That plants are affected by the intensity of illumination is shown by the fact that many plants will not grow under the shade of others. When in shade, they cannot manufacture enough sugar to keep them alive. For this reason it is not advisable to grow crop plants too close together, as they then shade each other, with the result that the plants are not as vigorous as they should be.

On the same plant the leaves which are fully exposed to the sun are thicker than those grown in the shade. This difference in thickness is of advantage, because when the light is strong sufficient light for photosynthesis will penetrate through a thicker layer of tissue than would be the case if the light were weak. Fig. 48 shows sections of two leaves from the same plant. The one on the right was fully exposed to the sun, while the other was more or less shaded. The leaves of many plants, if grown in different habitats, show much greater differences than those represented in this illustration.

Utilization of light. Not all portions of the spectrum are equally efficient in promoting photosynthesis. The light which is most effective is the red. To a considerable extent photosynthesis is also due to the blue-violet part of the spectrum. This latter light is less effective than the red because it furnishes less energy.

In photosynthesis a leaf actually makes use of only a very small part of the light which reaches it. Calculations of this amount vary. One high authority has estimated that the amount is not over one per cent of the light received by the leaf. Large quantities of water are evaporated from the leaf in the process of transpiration; energy is employed in changing this water into water vapor; perhaps half or more of the light which reaches the leaf is used up in producing this energy. A considerable proportion of the light that reaches a leaf is reflected from the surface or passes through the leaf and is lost.

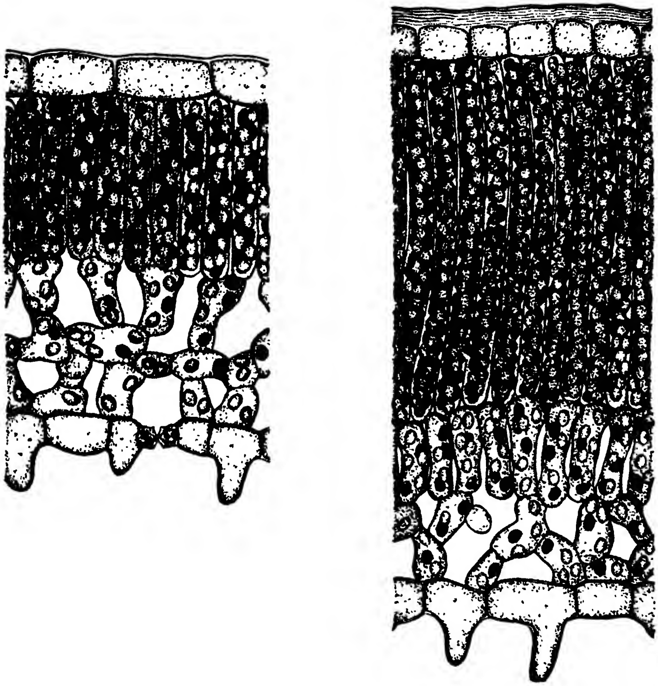

FIG. 48. Cross section of a shade leaf (left) and of a sun leaf (right) of a rain tree (*Enterolobium saman*). (× 485.) See Fig. 125

Temperature. Some plants may carry on photosynthesis at temperatures below zero centigrade. At such low temperatures the rate of photosynthesis is very low. With temperatures below about 10° C., increases in the temperature greatly increase the rate of photosynthesis. Increasing the temperature from ten to twenty degrees centigrade about doubles the rate. In a very carefully controlled experiment, increasing the temperatures from 20° C. to 30° C. multiplied the rate of photosynthesis by 1.6. Probably the best temperature for the average plant is between 25° C. and 30° C.

Energy. In photosynthesis, energy derived from light is used in the liberation of oxygen. It is a fundamental principle in physics that energy is not destroyed, but that one form of energy may be changed to another, as when electricity is transformed into heat. The energy from the light that is used in photosynthesis is therefore not destroyed but is stored in the resulting products as potential energy. All that is necessary to release this energy is to combine the compounds resulting from photosynthesis with the amount of oxygen that was liberated in photosynthesis, and thus change them back into carbon dioxide and water. We may say, in general, that energy is used in separating oxygen from carbon or hydrogen, and liberated in combining oxygen with carbon or hydrogen. The combining of oxygen with another substance is known as *oxidation*.

When we burn wood to produce heat or light, we make use of the fact that energy is liberated in oxidation. Wood is composed largely of compounds containing carbon and hydrogen. The burning of the wood is the oxidation of these compounds, with the production of carbon dioxide and water and the liberation of energy in the form of heat and light. The energy that is released is the energy that was derived from sunlight and stored in the process of photosynthesis. Coal consists of the remains of plants, and the burning of coal releases energy derived from sunlight and stored by plants in past geological ages. Oil is derived from plants or animals or their remains, and the energy released in the combustion of oil is also the stored energy of sunlight. We thus see that all the energy obtained by combustion and used for industrial purposes is the energy of sunlight stored by plants in the process of photosynthesis.

Plants and animals use their food not only as building materials out of which their tissues are constructed, but also as a source of energy. This energy, like that obtained by burning wood or coal, is liberated by oxidation.

ELABORATION OF PRODUCTS OF PHOTOSYNTHESIS

The sugar produced by photosynthesis is the basis from which the plant elaborates all the organic materials of which it is composed. These include substances which take part in the actual building up of the plant, including the protoplasm and the cell walls, and also substances which are stored as reserve food materials. The principal organic materials found in plants belong to three classes: carbohydrates, fats, and proteins.

When a plant manufactures more food than it needs for immediate use, the surplus is stored for future use. Food may be stored in certain parts of ordinary stems and roots; in especially modified stems, as in the potato and ginger; in modified roots, as in sweet potatoes; or in modified leaves, as in the onion. Seeds almost always contain a large amount of stored food, which nourishes the young plants until they become established. Reserve foods are stored as carbohydrates, fats and oils, and proteins.

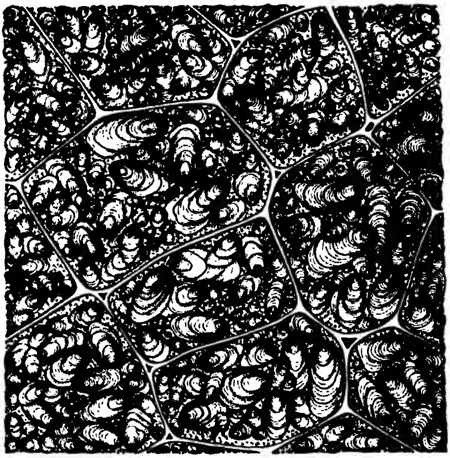

FIG. 49. Section showing a few cells of a potato tuber

The cells contain large and conspicuous grains of starch and a small amount of small granules of protein. (× 156)

Carbohydrates. Carbohydrates are organic compounds composed of carbon, hydrogen, and oxygen, the hydrogen and oxygen usually being in the same proportion as in water. In general the natural carbohydrates contain in each molecule six, or some multiple of six, carbon atoms. The simple carbohydrates have a sweet taste and are known as sugars.

The most important carbohydrates in plants are cellulose, of which cell walls are composed, and sugars and starches. The chief forms of carbohydrates in which food is stored are starches and sugars. Other storage forms of carbohydrates are hemicellulose, or reserve cellulose, and inulin.

Sugars. The three sugars that are found most abundantly in plants are *glucose* (grape sugar), *fructose* (fruit sugar), and *sucrose* (cane sugar). Glucose and fructose have the formula $C_6H_{12}O_6$. They are thus composed of the same kinds of atoms in the same proportion, but the arrangement in the molecule is different. The simplest natural sugars have this formula and are known as monosaccharides. Sucrose ($C_{12}H_{22}O_{11}$) has twice as many carbon atoms and is a disaccharide. It may be regarded as composed of one molecule of glucose and one of fructose, which are linked together with the dropping out of one molecule of water. Sucrose is familiar as the ordinary granulated sugar of commerce, which is obtained from sugar cane or sugar beets. Maple sugar also is sucrose. Glucose and fructose are found in nearly all plants, and glucose is an ingredient of a thick sirup which is made by treating starch with dilute sulphuric acid and afterward removing the acid. Such sirups are frequently called corn sirups, because corn starch is most commonly used in their preparation. As glucose and fructose are in solution and have relatively simple molecules, they are good material for the building up of other substances or for the furnishing of energy. In some plants, as in the sugar beet and sugar cane, sucrose is the chief form in which reserve food is stored.

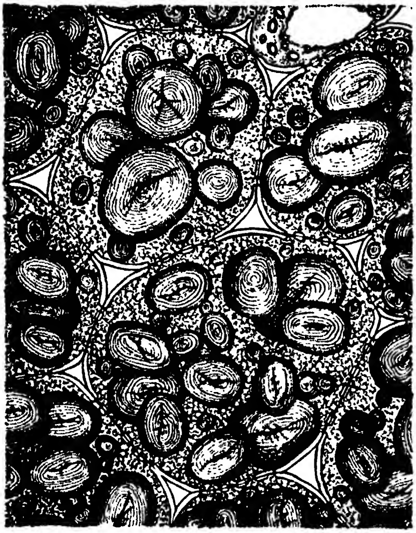

Fig. 50. Section of a few cells of mungo bean (*Phaseolus radiatus*)

The cells contain large and conspicuous grains of starch and small granules of protein. (× 270)

Starch. Starch is a polysaccharide having the general formula $(C_6H_{10}O_5)_n$, in which n is a large number. Just as sucrose may be regarded as the union of two monosaccharide molecules with the elimination of one molecule of water, so starch may be regarded as the union of many monosaccharide molecules with the loss of water. Starch is insoluble in cold water, and occurs in plants in the form of grains (Figs. 45, 49, 50). Starch grains from different plants have different shapes and configurations. Owing to this fact it is possible to identify starches by the use of a microscope. The grains of starch are found in amyloplasts (Fig. 51). Starch is formed from sugar, and can easily be converted into sugar either in plants or in a chemical laboratory. The storage of carbohydrates in the form of starch has the advantage that the starch is insoluble and therefore does not produce excessive osmotic pressure.

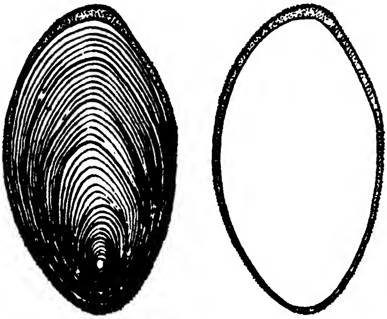

Fig. 51. Single grain of potato starch within an amyloplast (left) and amyloplast with grain of starch removed (right). (× 765)

Inulin. Inulin, like starch, is a polysaccharide and belongs to the general class of starches. In some plants, especially the *Compositae*, inulin occurs in considerable quantities. Inulin is soluble in water and occurs in plants in solution. It can be precipitated by alcohol, when it forms characteristic spherocrystals (Fig. 52). After being extracted from plants it is a white powder like starch in appearance.

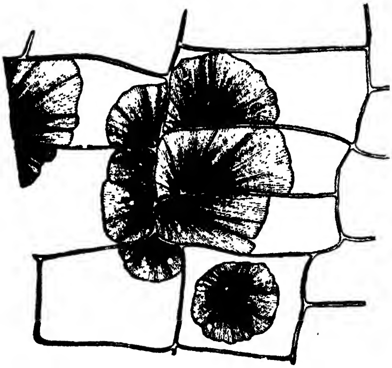

Fig. 52. Spherocrystals of inulin in cells of dahlia root. (× 304)

Hemicellulose. In some seeds food is stored in thickened cell walls in the forms of hemicellulose, or reserve cellulose. Food is stored in this form, however, much more rarely than as sugar or starch. Reserve cellulose is found in some palm seeds and also in the seeds of some other plants (Figs. 14, 53, 54).

Cellulose. Cellulose is a carbohydrate with a general formula similar to that of starch; that is, $(C_6H_{10}O_5)_n$. However, the atoms are arranged differently in the molecule, and starch and cellulose have very different properties. In the plant, cellulose is made from sugars. It serves as building material in the formation of the cell wall. There is no evidence that plants can convert true cellulose into a soluble form. There are, however, bacteria which can do this.

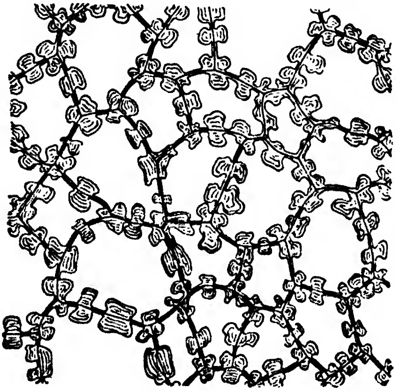

FIG. 53. Thickened walls of hemicellulose from betel-nut palm seed. (× 140)

Fats and oils. The natural fats and fatty oils in plants and animals all belong to the same general class of compounds and are composed of glycerin ($C_3H_5(OH)_3$) in combination with organic acids. Glycerin has three OH groups which can be replaced by acid radicals. In natural fats all three groups are replaced, so that the natural fats are triglycerides. Fats are composed of carbon, hydrogen, and oxygen, and are characterized by a small percentage of oxygen, as may be seen from the formulas of such common fats as stearin ($C_{57}H_{110}O_6$), palmitin ($C_{51}H_{98}O_6$), olein ($C_{57}H_{104}O_6$), and linolein ($C_{57}H_{98}O_6$). Owing to the very small percentage of oxygen contained in fats, the oxidation of fats produces large amounts of energy. More energy is obtained by oxidizing a given volume of fats than by oxidizing a similar volume of any other known kind of compound that is found in either plants or animals.

Fats may be solid or liquid (oils), according to the temperature. Fatty oils occur in plants in the form of globules (Figs. 55–58).

Proteins. The proteins are the most important group of compounds found in plants, as they constitute the active matter of protoplasm, and the chemical phenomena of life processes are associated with them.

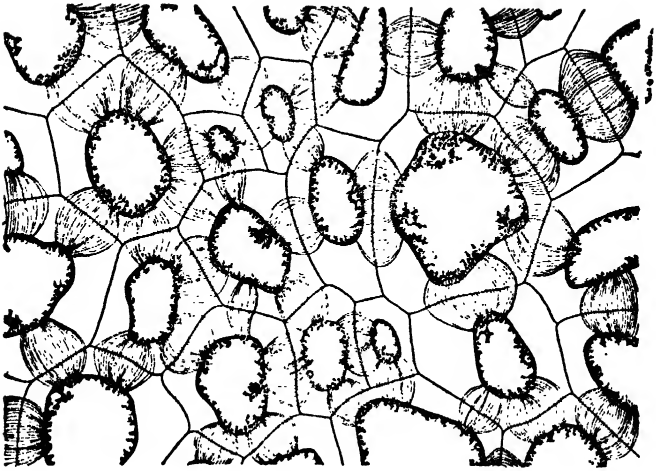

Fig. 54. Reserve cellulose in the form of thickened cell walls in the seed of the Japanese persimmon (*Diospyros kaki*)

The white areas around the cells are the cell walls. Note the fine protoplastic connections between the cells

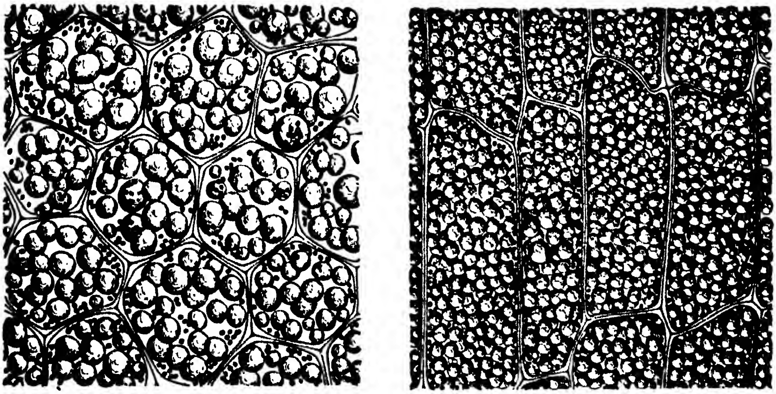

Fig. 55. Cells of endosperm (meat) of coconut

Left, cut parallel with the surface of the meat (× 290); right, cut perpendicular to the surface of the meat (× 185). The large globules are oil and the small granules are protein

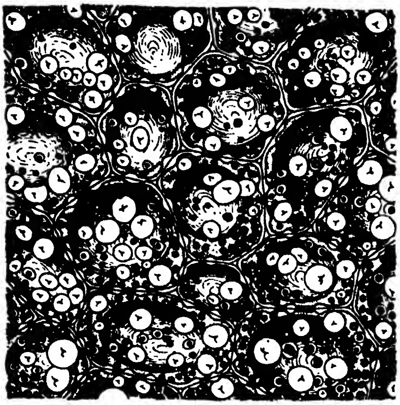

Fig. 56. Cells near the outer part of the cotyledon of peanut

The large globules are oil; the white bodies, starch grains; the small dark granules, protein; and the knoblike thickenings on the walls, hemicellulose. (× 225)

Proteins are exceedingly complex compounds, as will be seen from formulas which have been calculated for such representative proteins as zein

$$(C_{736}H_{1161}N_{184}O_{208}S_3)$$

from Indian corn; gliadin

$$(C_{685}H_{1068}N_{196}O_{211}S_5)$$

from wheat; casein

$$(C_{708}H_{1130}N_{180}O_{224}S_4P_4)$$

from milk. The proteins contain carbon, hydrogen, oxygen, nitrogen. Other substances, such as sulfur and phosphorus, are also found in some proteins. Proteins are not only the principal constituents of protoplasm but, in the form of solid granules, are frequently found in plants as reserve food material.

Proteins are formed by a rearrangement of the atoms of carbohydrates with the addition of nitrogen, commonly sulfur, and sometimes phosphorus. Proteins are divided into two classes, simple proteins and conjugated proteins. The simple proteins are made up of about twenty substances known as amino acids. These are in themselves very complex, and a molecule of protein contains many molecules of amino acids. Amino acids are peculiar in that they have both basic and acid properties.

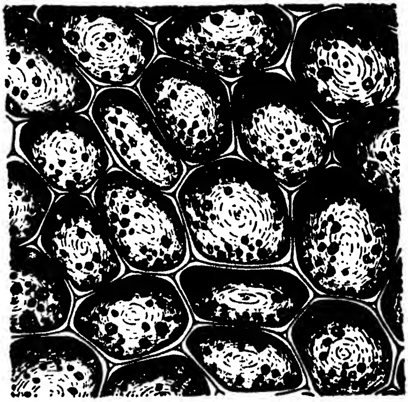

Fig. 57. Cells of lumbang nut

The granules are protein. Note how the oil fills the cells. Lumbang is a fair-sized tropical tree. The oil has much the same properties as linseed oil. (× 265)

The proportion of the different amino acids in different proteins varies; and some proteins lack amino acids found in other proteins. Animal proteins are better for human food than plant proteins because the amino acid content of animal proteins is more like that of human proteins than is the amino acid content of plant proteins. Some plant proteins lack entirely some of the amino acids which are essential for the building of human proteins.

Conjugated proteins are proteins which are united with other material. The proteins in the nucleus are mostly nucleoproteins. These are compounds of nucleic acid and proteins. Nucleic acid is a very complex compound and contains phosphorus.

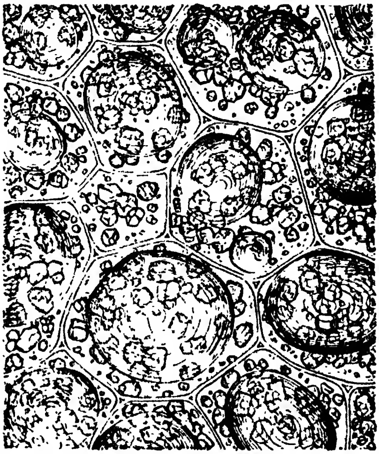

Fig. 58. Cells from seed of *Croton tiglium* with large, rounded oil globules and irregularly shaped protein granules. (× 450)

Plant materials as human food. The sugars, starches, fats, and proteins which are stored in plants are also used as food by man and animals. The fats and carbohydrates are sources of energy. In man they may be digested and then stored as fat. They are not used as body-building material, as the human organism cannot build proteins except from proteins. Plant proteins serve human beings as sources of both energy and body-building material. People need much more protein if taken in the form of plant proteins than if consumed as animal proteins. This is because, as mentioned above, some of the amino acids which are necessary to human nutrition and cannot be manufactured in the human body are lacking in some of the plant proteins, and, moreover, the proportion in which amino acids occur in plant proteins is not as favorable for human nutrition as the proportion in animal proteins. The parts of plants which furnish the greatest amount of food are the storage organs where the plant has stored food for the use of itself or its progeny. Most seeds are rich in reserve food material, and seeds furnish most of the energy foods of a large part of the human race. Food in seeds, however, is not always in a form suitable for human use. This is true of date and persimmon seed, where the food is stored largely as hemicellulose. Other seeds contain poisonous materials or substances which render them unpalatable. Fruits usually contain less nutritive material than seeds; here the food is stored to attract animals which scatter the seed, and not for the use of the plant itself.

People need large quantities of calcium and iron. These are found in vegetables and fruits; they are particularly abundant in green leafy vegetables, and very much less abundant in blanched leaves. In their importance as sources of calcium and iron the green leafy vegetables rank first, other succulent vegetables second, and fruits third.

Vitamins. Plants are very excellent sources of vitamins. Vitamins are substances which are very essential in animal and human nutrition. In most cases, if not in all, the vitamin or a substance which is readily converted into vitamin is manufactured by plants, and cannot be manufactured in the animal body. There are several vitamins which are very widely distributed in plants and in which human diet may be deficient. Vitamins are usually distinguished by letters. Plants are excellent sources of vitamins A, B, C, and G. Vitamin A is formed from carotin, one of the pigments of chlorophyll. It is generally regarded as essential for giving immunity against infection and for the prevention of certain types of eye trouble. As carotin is one of the pigments of chlorophyll, it follows naturally that the green leafy vegetables are excellent sources of vitamin A. The color of many yellow or highly colored vegetables and fruits, such as carrots, yellow corn, yellow sweet potato, tomatoes, cantaloupes, oranges, and pineapples is to a considerable extent due to carotin, and these are good sources of vitamin A. Vitamin B is necessary for normal growth. It is known as the antineurotic vitamin, and a deficiency results in the disease called "beriberi." Vitamin B is very widely distributed in both vegetable and animal products, but is insufficient in polished cereals. Beriberi is found chiefly in the Orient among people whose diet consists largely of polished rice. Vitamin C is necessary for the normal functioning of the body, and deficiency results in scurvy. This vitamin is abundant in many fruits and vegetables, but is destroyed to a considerable extent by cooking in the presence of oxygen. This is one of the reasons that fresh fruits are valuable, as they contain vitamin C and they are eaten without cooking. Vitamin G is widely distributed in fruits and vegetables. It is necessary for normal growth and well-being, and a considerable deficiency results in the disease known as pellagra. A pronounced deficiency of a vitamin results in a specific disease. A lesser deficiency may result in a decrease in well-being without producing very pronounced symptoms. The actual amounts of vitamins present in plants are small. The amount needed by men and animals is correspondingly small. Small amounts have very pronounced effects. There is practically no evidence as to the role played by vitamins in the activity of a plant.

DIGESTION

Food stored as starch, cellulose, fatty oil, or protein is not soluble in water, and so must be converted into a soluble form before it can be used by plants or transported from one part of a plant to another. This conversion is accomplished by substances known as *enzymes*, which belong to the general category of catalysts. *Catalysts* are substances which change (usually accelerate) the rate of a reaction. Owing to the fact that a reaction which is accelerated by an enzyme might take place so slowly without the enzyme as to be imperceptible, it is customary, in order to avoid the use of cumbersome language, to speak of an enzyme as acting on a substance rather than as accelerating the rate of a reaction.

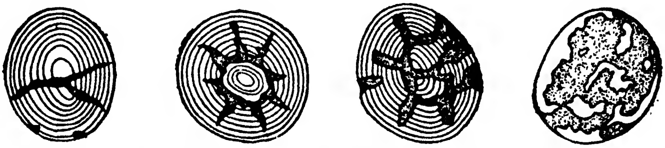

FIG. 59. Stages in digestion of starch grains of barley by diastase

Enzymes, like other catalysts, are characterized by not being a part of the initial substance in the reaction or of the final product, by not changing in the reaction, by influencing a change in a relatively great volume of the reacting substance, and by accelerating the effect in direct proportion to the amount of catalyst present.

As an example of inorganic catalysts we may mention spongy platinum, which accelerates the oxidation of sulphur dioxide in the manufacture of sulphuric acid. Another example is finely divided nickel, which is used in the commercial hydrogenation of oils. By this means many liquid oils are turned into solid fats.

Plants contain many different kinds of enzymes, and each enzyme acts on only one substance or on a group of similar substances. The best-known reactions that are accelerated by enzymes are those in which complex substances are split into simpler ones. It is known in some cases, however, that a given enzyme can accelerate a reaction in either direction; that is, the enzyme which splits up a complex substance can also influence the reverse process of the building up of the same complex substance.

For simplicity we will mention only a few of the many known enzymes. *Diastase* converts starch into sugar, so that the action of this substance changes an insoluble substance into a soluble one (Fig. 59). *Invertase* changes cane sugar into glucose and fructose. *Lipase* breaks up fats into their components, glycerin and fatty acids. *Papain* splits proteins into amino acids.

Enzymes are just as important in animals as in plants. The process of digestion could not be carried on in their absence.

The chemical composition of enzymes is entirely unknown, and they can be recognized only by their action; but, since many of them have been prepared as dry powders, they may be regarded as chemical compounds the composition of which we may hope to know some day.

Enzymes are colloids, and, like colloids in general, are unstable. Temperature affects enzymic action in much the same way as it does vital processes. Very little enzymic activity takes place at temperatures around 0°C. At favorable temperatures, the rate of enzymic activity is about doubled with an increase in temperature of 10°C. The optimum temperature for enzymic activity is usually between 45°C. and 50°C., and so is higher than that of vital activities such as growth. Heating to 70°C. destroys enzymes.

ASSIMILATION IN HETEROTROPHIC PLANTS

Plants which manufacture their own food are autotrophic plants. There are various types of algae which have pigments in addition to chlorophyll and are also autotrophic; that is, they manufacture their own food. In addition there are autotrophic bacteria. Some of these obtain energy by oxidizing inorganic substances. The processes concerned will be discussed in the chapter on bacteria.

Many plants lack chlorophyll and are dependent on organic compounds as a source of food material and energy. Such plants are heterotrophic. They are saprophytes (Fig. 9) when they obtain their nutriment material from dead organic matter, and parasites (Figs. 7, 8, 60, 61, 62) when they subsist on living plants or animals. The nutrition of heterotrophic plants is often not very different from that of the colorless parts of green plants which must obtain their food from the green portions of the plant.

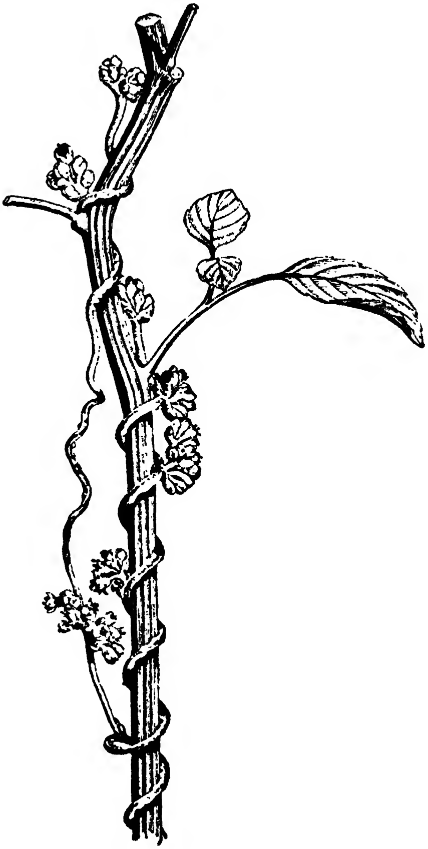

FIG. 60. *Cuscuta*, a parasitic vine

The stems produce haustoria that enter the host and absorb water and food material. These haustoria are regarded as roots by some authorities. (× 1)

Saprophytes. Saprophytes include a very large number of mushrooms and molds. When green plants use food stored in them, this food is first converted into soluble form by enzymic action. The enzymes concerned are secreted within the tissues of the plant itself. Saprophytes, such as molds, excrete enzymes into the medium in which they grow and in this way convert insoluble materials into soluble ones which they can absorb. Most saprophytes, when supplied with energy-producing materials, can utilize simple inorganic nitrogenous compounds for the building up of proteins just as green plants do. Some bacteria require nitrogen in organic form, and these are very like animals in their nutrition. On the other hand, there are certain types of bacteria which can utilize the nitrogen of the atmosphere. These plants are exceedingly important from the standpoint of agriculture and will be discussed later.

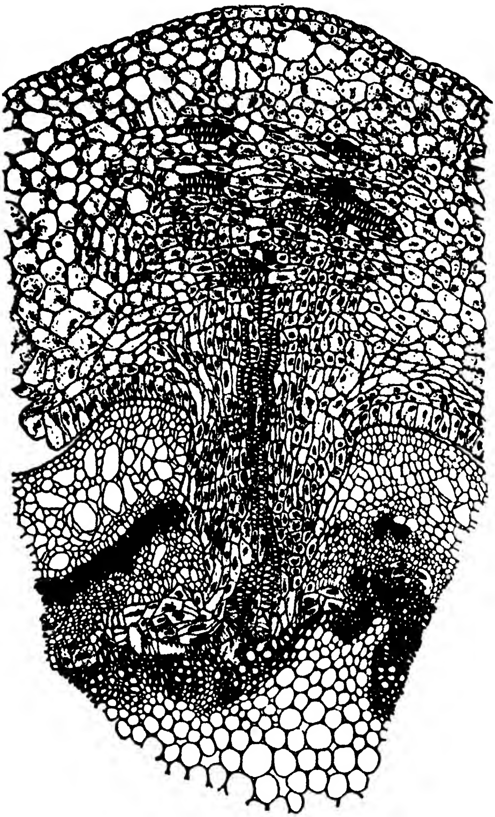

FIG. 61. Section through haustoria and portion of host of *Cuscuta* (see Fig. 60)

Note that cells of the haustorium are between the xylem and the phloem of the host, and that the xylem of the parasite is in contact with that of the host. (× 70)

Parasites. Many parasites live much as do saprophytes except that they are attached to living organisms from which they obtain food. Figs. 60, 61 show the relation of the well-known parasite *Cuscuta* (dodder) to the host. The stem produces haustoria which enter the host. In Fig. 61 it will be seen that the cells of the haustorium are between the phloem and the xylem of the stem of the host, and so are in a favorable position to absorb both food and water. The xylem of the haustorium is in contact with that of the host. It can be recognized by the spiral thickenings on the walls. Some plants, such as the mistletoe (Fig. 8), are abundantly supplied with chloroplasts, and their chief dependence on the host is for water, though they must also depend on it for those other elements which autotrophic plants derive from the soil. Such plants are known as hemiparasites.

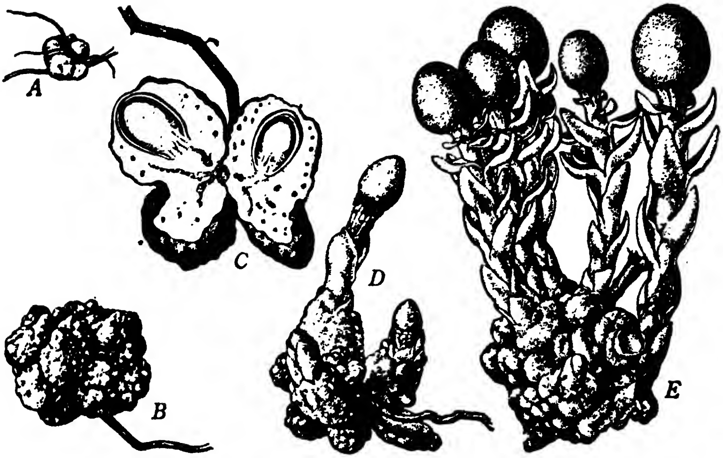

FIG. 62. Development of *Balanophora*, a parasite growing on the roots of other plants

When the germinating seedling of the parasite reaches the host, it develops a large tubercle (*A*), and the cortex of the root of the host is destroyed where the tubercle is in contact with it. The wood becomes broken up and the strands separated from each other. The tissues of the parasite penetrate between those of the host to such an extent as to make it difficult to distinguish between host and parasite. The development of the parasite results in the death of the root of the host beyond the point of attachment (*B*). The flowering shoots of the parasite develop within the tubercular growth and, in expanding, break through it. *C* shows a section of the tubercular growth enclosing two developing flower shoots. The rounded structures at the ends of the shoots are flower heads. *D* and *E* show more advanced flower shoots. (After Kienholz)

INSECTIVOROUS PLANTS

There are several genera of flowering plants which have leaves that catch insects and other small animals and absorb nutriment material, particularly nitrogenous substances, from them. In some cases the captured animal is decomposed by bacteria, in others it is digested by the enzymic action of digestive fluids secreted by the leaves themselves. All these plants are provided with chloroplasts, and probably all of them can live in a purely autotrophic manner when animal food is not available.

Pitcher plants. The pitcher plants have their leaves modified into pitchers in which water collects. The best-known pitchers belong to the temperate-zone genus *Sarracenia* (Figs. 63, 64) and the tropical genus *Nepenthes* (Fig. 65). The species of *Sarracenia* are rosette plants; that is, the leaves arise in a cluster from a very short stem. The species of *Nepenthes* are vines on which the pitchers are borne at the ends of long, tendril-like leaves. Insects are drowned in the water in the pitchers. In the pitchers of the genus *Sarracenia* the insects are decomposed by the action of bacteria, while the pitchers of the genus *Nepenthes* excrete a digestive fluid. After the insects are decomposed, the products are absorbed by the leaves. The pitchers of *Nepenthes* frequently collect so much clear water that it can be used by people for drinking. In such cases it would seem probable that the leaves not only furnish the plants with materials from the bodies of the captured insects but also with water.

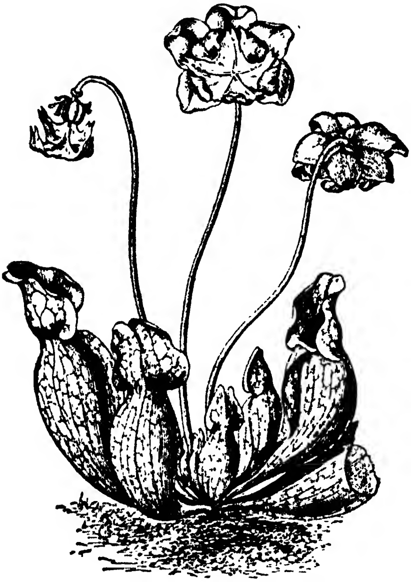

Fig. 63. *Sarracenia*, a pitcher plant, showing flowers and pitcher leaves. Modified after Barton

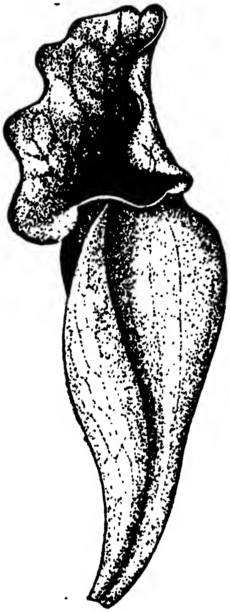

Fig. 64. Pitcher leaf of *Sarracenia*. (× $\frac{2}{3}$)

Sundews. The sundews (*Drosera* spp.) are small plants which have their leaves arranged in the form of a rosette (Fig. 66). These leaves are thickly covered with glands which are borne on slender stalks (Fig. 67). These glands excrete a sticky fluid in which insects become entangled when they come in contact with the leaf. After an insect has been captured in this manner, the leaf encloses it while the glands excrete a fluid which digests the insect. The digested material is then absorbed by the leaf.

Venus's-flytrap. The Venus's-flytrap (*Dionaea muscipula*) is also a small rosette plant (Fig. 68). The petiole is expanded into a bladelike structure which serves for photosynthesis. The blade is specially fitted for capturing insects. It consists of two valves, each of which bears upon its upper surface three short, rather stiff bristles. Mechanical contact with these bristles causes the two valves to close together. When an insect alights on the blade and brushes against these bristles, the leaf closes and thus entraps the insect. The glands on the surface of the blade then excrete a fluid which digests the insect, after which the digested material is absorbed and the leaf opens.

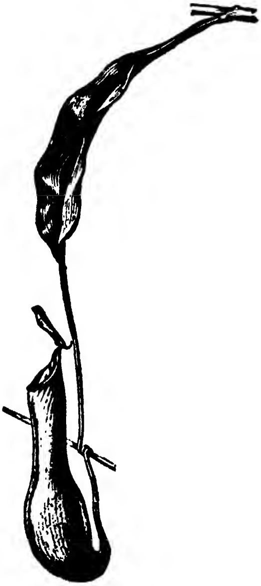

Fig. 65. **Pitcher leaf of** ***Nepenthes.*** **(× ¼)**

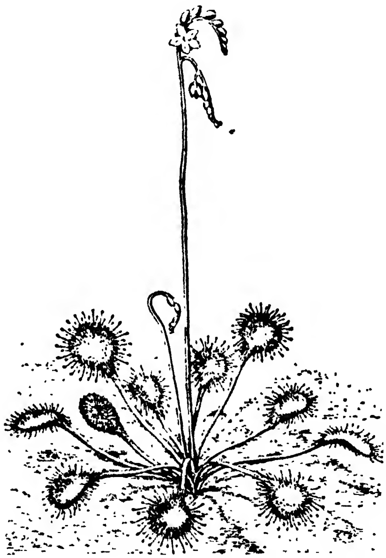

Fig. 66. ***Drosera*****, a carnivorous plant. (× ½)**

Utricularia. Plants of the genus *Utricularia*, some of which are submerged aquatics, are provided with bladders that entrap small animals in very much the same way as an ordinary trap catches a rat (Fig. 69). These bladders are provided with trap doors which allow the animals to enter and then bar their exit (Fig. 69). Small crustaceans may remain alive in these bladders for a considerable length of time, and it is probable that some of the products of their excreta are absorbed by the plant. They finally die and are decomposed by the action of bacteria. Nitrogenous products, which can be absorbed by the plants, are thus liberated.

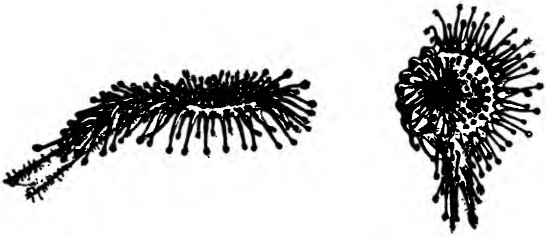

FIG. 67. Leaves of *Drosera*. (Redrawn after Darwin)

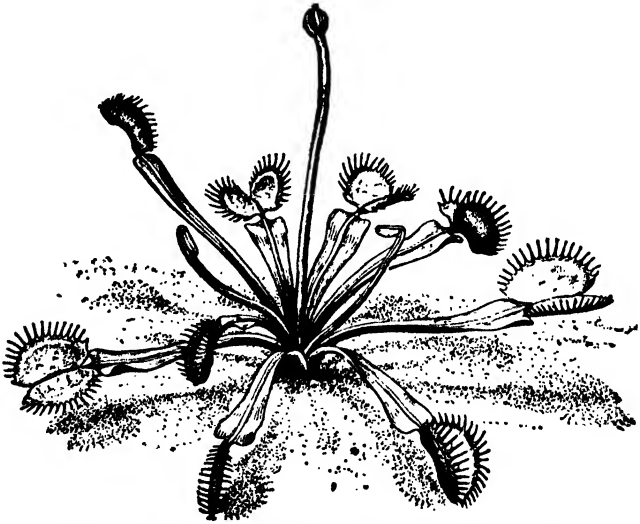

FIG. 68. Venus's-flytrap (*Dionaea muscipula*). (× ⅔)

Some species of *Utricularia* live in water (Figs. 69, 70), while others grow on a very moist substratum (Fig. 71). The latter have aërial shoots which bear flowers. In some forms there are ordinary leaves near the base of the plant, and also structures (Fig. 71) which are morphologically leaves but which have the appearance of horizontal branches and bear leaflike outgrowths and also animal-catching bladders. These branchlike leaves serve the purposes of roots, both in anchoring the plant and in absorbing water.

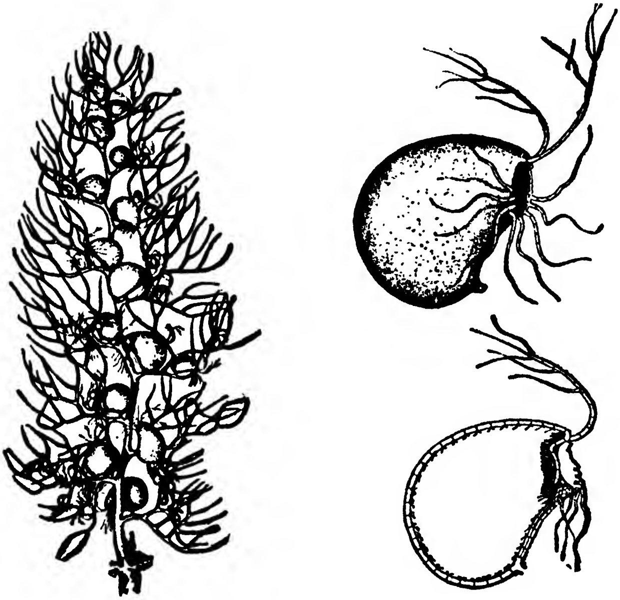

FIG. 69. *Utricularia*

Left, portion of a plant (× 1); upper right, an animal-catching bladder (× 5); lower right, section of animal-catching bladder (× 5)

There are other forms of carnivorous plants, but those already mentioned will give some idea of the diversity of leaf structures used in capturing small animals.

Similarity to animals. Some carnivorous plants have properties which are usually regarded as characteristic of animals. The case of *Dionaea* is particularly striking. This plant is able to respond to stimuli by movement, to excrete a digestive fluid and to digest animals, and then to absorb the products of digestion. Such cases serve to emphasize the fundamental similarity between animals and plants.

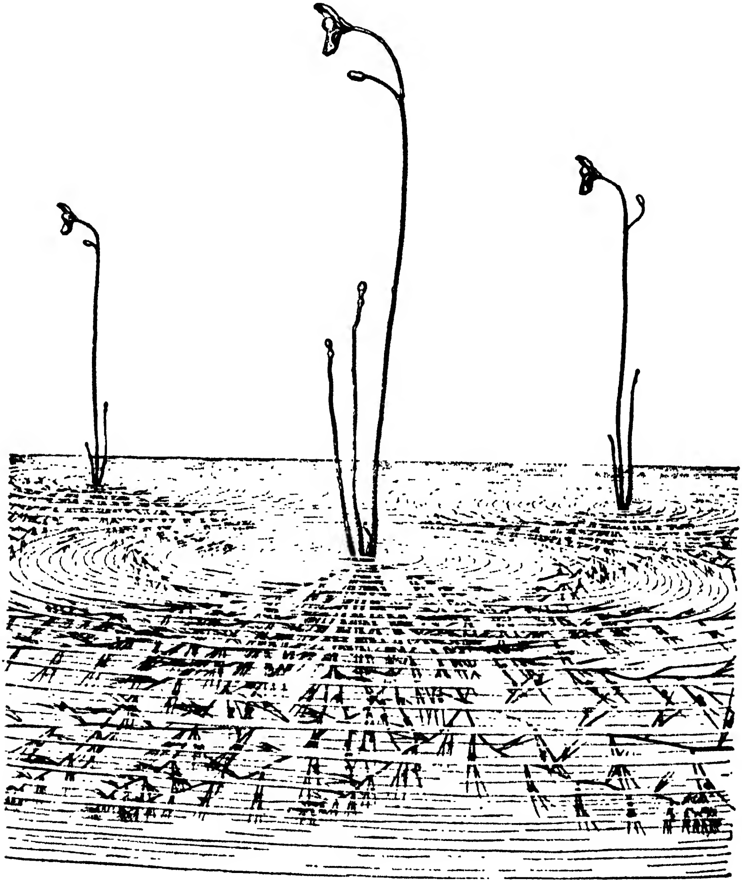

Fig. 70. Habit of floating *Utricularia*

As the insectivorous plants can manufacture food by means of photosynthesis and can make use of inorganic nitrogen compounds for the synthesis of proteins, their method of nutrition is nothing like so near that of animals as is the case with some bacteria which must obtain all their food in the form of organic compounds.

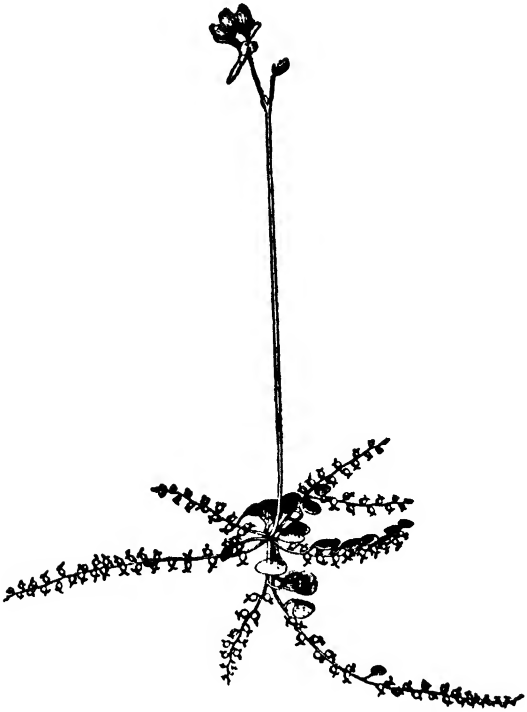

Fig. 71. A *Utricularia* that lives on a very moist substratum

The horizontal stemlike structures are modified leaves which bear leaflike outgrowths and animal-catching bladders and function as roots. (× 1)

RESPIRATION

Definition. The oxidation by plants or animals of compounds containing carbon and hydrogen to carbon dioxide and water, with the liberation of energy, is known as respiration.

Importance. The value of the process lies in the fact that it releases the energy of sunlight which was stored by the leaves in photosynthesis, so that this energy may be used for the vital activities of the plant.

All work requires energy. Moreover, the energy must be in a form suitable for the performance of the particular kind of work to be done. In the flowing of water in a large waterfall a tremendous amount of energy is expended. This energy can be used for cooking or illuminating, but in order that this may be done the form of the energy must be changed to heat or light.

In the activities of a plant, work is performed; and, like all other work, this requires energy. The green parts of plants use the energy of sunlight for photosynthesis, but energy as it occurs in light is not in a form that can be used for such vital processes as growth, movement, etc. It becomes converted into suitable form for these processes, however, when, after being stored in photosynthesis, it is released by respiration.

In this way not only is the energy of sunlight changed to a form in which it can be used for the general vital activities of the plant, but, moreover, any excess which is stored in the products of photosynthesis and not needed at the time may be conserved for use when it is required.

Process. Respiration is not a particular function of any plant organ but is carried on by all living cells. In this process oxygen is combined with compounds containing carbon and hydrogen. This results in the breaking down of the compounds to form carbon dioxide and water, and in the liberation of energy.

If sugar is the compound that is being oxidized, we may write the formula for respiration as follows:

$$C_6H_{12}O_6 + 6\ O_2 \longrightarrow 6\ CO_2 + 6\ H_2O.$$

If we compare the above formula with that previously given for photosynthesis, we find that one is the reverse of the other, which is in keeping with the fact that photosynthesis stores energy, while respiration releases it.

This oxidation process is carried on at ordinary temperatures. The oxidation at such temperatures is due to the activity of oxidizing enzymes.

Source of oxygen. In leaves that are carrying on photosynthesis, oxygen which is liberated by this process is used in respiration. If photosynthesis is rapid, however, more oxygen is liberated than is used in respiration, and the excess diffuses from the cells into the intercellular spaces and thence into the external atmosphere. This is the case under ordinary conditions in bright light.

Plant organs which do not contain chlorophyll, such as petals and roots, obtain oxygen from the air. The same is true of leaves when they are in the dark and so are not liberating oxygen by means of photosynthesis. In this case oxygen in the intercellular spaces goes into solution in the water held in the cell wall. It then diffuses in this water until it enters the protoplasm, where it can be used for respiration.

Fate of products. The water produced by respiration mixes with the water of the cell.

In the case of organs without chlorophyll or of green organs in the dark, the carbon dioxide diffuses out of the cell into the surrounding atmosphere. In green tissues which are actively carrying on photosynthesis most of the carbon dioxide will be used in photosynthesis without leaving the cell in which it is produced.

From the above it will be seen that when a plant organ, from lack of chlorophyll or light, is not carrying on photosynthesis, it will, owing to respiration, absorb oxygen and give off carbon dioxide. When photosynthesis is active in green tissues, more oxygen is liberated by photosynthesis than is used in respiration, and more carbon dioxide is employed in photosynthesis than is produced by respiration, with the result that these tissues will absorb carbon dioxide and give off oxygen.

Whether leaves in light give off carbon dioxide or oxygen will naturally depend on whether more carbon dioxide is produced by respiration or is used in photosynthesis. With very feeble light the respiration of leaves may produce more carbon dioxide than is used in photosynthesis, and so the leaves absorb oxygen and give off carbon dioxide even when they are performing photosynthesis slowly. On an average day, however, the products of photosynthesis must be built up in the green tissues much more rapidly than they are broken down by respiration. A surplus must be accumulated to supply material for the respiration of the organs lacking chlorophyll, and also for the respiration of the green tissues themselves at night. In addition, building material must be produced for the growth of the plant body.

Demonstration. If germinating seeds are inclosed in a vessel containing ordinary air, it will be found that the oxygen is absorbed and replaced by carbon dioxide. The same phenomenon can be shown by using green plants if they are kept in the dark.

A very simple method of demonstrating the exchange of gases in respiration is that shown in Fig. 72. A few germinating seeds are placed in the bottom of a test tube and held in place by a small amount of cotton. The test tube is then inverted over a solution of potassium hydroxide. The carbon dioxide that is given off by the seeds is absorbed by the solution, so that as oxygen is taken up the solution rises in the tube. This experiment can be checked by placing germinating seeds in another tube and inverting the tube over mercury, which does not absorb carbon dioxide. The mercury will not rise in the tube, because the oxygen that is taken up by the seeds is replaced by carbon dioxide, and, as the latter is not absorbed by the mercury, the volume of gas is not decreased. A green leaf can be used in place of the seeds in this demonstration if the preparation is kept in the dark.

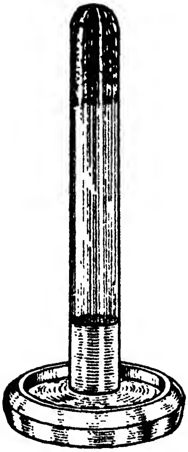

Fig. 72. Method of demonstrating respiration of seed

Heat is produced by respiration. This can be demonstrated by the arrangement shown in Fig. 73. A vacuum flask is partially filled with germinating seeds. A vial containing potassium hydroxide is also placed in the flask to absorb carbon dioxide. A thermometer is then inserted through the mouth so that the bulb is among the seeds. The mouth is now plugged with cotton, which allows air to enter the flask. The heat produced by respiration causes the mercury to rise in the thermometer. This experiment should be checked by setting up a preparation similar to the one just described except that the germinating seeds are replaced by dead ones. In the latter case the thermometer will not show a rise in temperature.

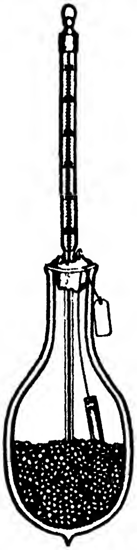

Fig. 73. Apparatus for demonstrating liberation of heat in respiration

Respiration in plants and animals. Respiration is fundamentally the same process in both plants and animals, and consists essentially in the liberation of energy by the oxidation of compounds containing carbon and hydrogen. The methods by which oxygen enters the body and carbon dioxide leaves it are very different in the higher groups of the two kingdoms; these processes, however, are only incidental to the fundamental one of oxidation. Also, the methods by which the materials to be oxidized are obtained are very different in green plants and in animals. The plants themselves manufacture these materials, while animals must obtain them, either directly or indirectly, from plants. These processes are, however, not a part of respiration.

Respiration is equally essential in plants and animals, as it is the source of energy for vital activities. When respiration ceases, there is no further supply of energy for these activities, and death ensues.

Oxygen supply. Since respiration is a process of oxidation, a plentiful supply of oxygen is one of the prerequisites for normal respiration. If the supply of oxygen is inadequate, respiration will be checked, and this will limit the rate of vital activities, such as growth, which are dependent on the energy liberated by respiration.

Plants will live for a time in an atmosphere that does not contain oxygen. In this case energy is obtained by a process known as *anaerobic* or *intramolecular* respiration. In anaerobic respiration, energy is liberated by the incomplete breaking down of carbohydrates. Carbon dioxide and, usually, alcohol are produced. Anaerobic respiration is less efficient than normal respiration. Much more material is broken down, and, as a rule, much less carbon dioxide is produced.

Sufficient oxygen is available for the aerial parts of plants, but this is not always true of roots and seeds in the ground. The soil should be porous and should contain air in the spaces between the particles. If there is so much water in the soil that it interferes with the diffusion of sufficient oxygen to the roots, the growth of the latter will be retarded. For this reason soil should be well drained. The roots of plants may be killed if the ground is flooded for a considerable length of time. The same thing may result if the level of the ground around a tree is raised until the roots are buried so deeply that sufficient oxygen does not reach them. Seeds respire actively during germination, and so will not germinate without a sufficient supply of oxygen.

Photosynthesis	**Respiration**
Uses carbon dioxide	Releases carbon dioxide
Releases oxygen	Uses oxygen
Uses and stores energy	Liberates energy
Builds up sugar	Breaks down sugar
Requires light	Does not require light
Requires chlorophyll	Does not require chlorophyll
Increases dry weight	Decreases dry weight

Metabolism. In this chapter we have studied the metabolism of the plant and have seen that it consists of two kinds of changes: the building up of complex substances from simple ones and the breaking down of the complex ones into simpler forms. In the building-up processes are formed all the various materials which go to make up the complex structure of the plant, and also those in which food is stored for future use as building material or for furnishing energy. In the breaking-down processes reserve materials may be converted into simpler ones to be built up again into integral parts of the plant, or they may be broken down into carbon dioxide and water to furnish energy for the varied activities of the plant.

CHAPTER VI

WATER IN RELATION TO LEAVES

HYDRATION

We have seen that a large part of the stiffness of leaves is due to water contained in their cells. The forces that hold water within the cell walls are not in the walls themselves but in the cell contents. The cell walls are very permeable to water; that is, water can pass through them very readily. If there were no forces in the cell contents to hold the water, the water would leak out through the walls. The term *hydration* may be used to denote the absorption and holding of water, without regard to the manner in which this is accomplished. The hydration of the cell contents is, then, the absorption and holding of water by the cell contents. This is due to two forces: the *hydration of colloids* in the cell and *osmotic pressure.*

Hydration of colloids. In the discussion of the colloidal nature of protoplasm, in the chapter on the cell, it was pointed out that many colloids are capable of hydration (that is, of absorbing and holding water) and that protoplasm contains hydrated colloidal particles. Protoplasm is capable of absorbing and retaining large quantities of water. When protoplasm absorbs water, it tends to swell and stretch the cell wall and thus give rigidity to the cell.

Osmotic pressure. When a substance is in solution, the dissolved substance tends to become equally distributed or *diffused* throughout the liquid (solvent) in which it is dissolved. This can be illustrated by the following example: If a small quantity of sugar is placed at the bottom of a vessel containing water, the sugar will go into solution and, even if there is no movement of the water, will become diffused throughout the water so that all of the water will have a sweet taste. *Diffusion* is very important in plant physiology, for by this means substances in solution in one part of a plant are frequently carried to other parts.

The force exerted by diffusion is called *osmotic pressure.* This force may be demonstrated by the use of a semipermeable membrane. A *semipermeable* membrane is a membrane through which the solvent can diffuse readily, but through which at least some of the substances which may be in solution cannot pass readily, if at all. Good examples of semipermeable membranes are animal bladders and the thin membrane around the white of an egg. When two solutions of unequal concentration are separated by a semipermeable membrane, diffusion still tends to produce an equal distribution of the dissolved substance throughout the solvent, and this results in the diffusion of the solvent from the less concentrated to the more concentrated solution. The solvent from the less concentrated solution accumulates in the more concentrated solution and dilutes it, and the tendency is for this process to continue until the two solutions have the same concentration.

The operation of a semipermeable membrane can be illustrated in the following manner: When a dilute solution of sugar in water is separated by a semipermeable membrane from a more concentrated solution of sugar in water, and the semipermeable membrane is such that water can pass through it readily while sugar cannot, the water from the dilute solution will diffuse into the concentrated solution, the tendency being for this diffusion to continue until the solutions on both sides of the membrane are of equal concentration. The operation of osmotic pressure through a semipermeable membrane may be expressed in general by saying that if two solutions are separated by a semipermeable membrane, the solvent from the less concentrated solution will tend to accumulate in the more concentrated one until the two solutions have the same molecular concentration. Diffusion through a semipermeable membrane is called *osmosis.*

The above experiment can be performed very easily with a thistle tube and a piece of parchment paper, which is a semipermeable membrane (Fig. 75). The paper is tied tightly over the large mouth of the bulb, the tube is inverted, and the bulb is filled with a sugar solution. The tube is now set in a dish of water with the tube end uppermost and the bulb about three-fourths immersed in the water. The sugar solution will absorb water and gradually rise in the tube.

Osmosis in plant cells. The outer layer of the protoplasm of a plant cell is somewhat modified and is known as the *plasma membrane.* This acts as a semipermeable membrane around the cell, while the protoplasm as a whole is a semipermeable membrane around the vacuole. These membranes are of such a nature that water passes through them readily, while some of the substances which are in solution pass less readily and some not at all. The solution in living cells is highly concentrated and is connected by means of the conducting tubes in the xylem with the roots, and through these with the water in the soil; this water is a dilute solution of mineral salts. By the forces of osmosis and hydration of colloids this water is drawn into the plant cells until the cell walls become stretched by the water. Cells that are thus stretched are said to be *turgid*, and the force of the stretching is called *turgidity.* This turgidity gives considerable strength to the cells, as was explained on page 37, just as a soft hose becomes hard when filled with water, or a bicycle tire extremely rigid when filled with air under pressure.

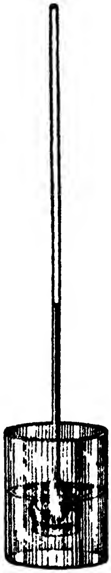

FIG. 75. Apparatus for demonstrating osmosis

If a cell is placed in a concentrated solution of sugar or of a mineral salt, this solution will pass through the cell wall and will draw water from the protoplasm. The removal of the water decreases the size of the cell contents so that the protoplasm is drawn away from the cell wall, as shown in Fig. 76. A cell in this condition is said to be *plasmolyzed.* If the plasmolysis has not gone too far, the removal of the concentrated solution and its replacement by a weak solution will allow the cell contents to absorb water and resume their original distribution. When fresh-water plants or the roots of land plants are placed in salt water, they are killed by plasmolysis.

Water may pass from cell to cell by means of osmotic pressure or the hydration of colloids. When a cell which is exposed to the air is losing water, the concentration of the dissolved substances in it is increased, so that it tends to draw water from a neighboring cell. This cell in turn may draw water from another cell. In this way water may be drawn from cell to cell until the source of supply is reached.

A semipermeable membrane may be of such a nature that some dissolved substances will pass through it readily, while others will do so slowly or not at all. Some dissolved substances pass more readily than others through the semipermeable membranes of plant cells.

Imbibition. The cell wall is composed of colloidal substances and, like colloids in general, has the property of absorbing water and swelling. This process is known as imbibition. Cell walls absorb water with tremendous force, as can be seen when dry wood absorbs water and swells. When a substance which is soluble in water, such as sugar, is placed in water, the attraction between the molecules of sugar and water is greater than the cohesive force of the sugar. The result is that the molecules of sugar are separated and go into solution. In the case of cell walls there is a strong attraction between the particles composing the walls and water, but this is not strong enough to overcome the force with which the particles of the cell wall adhere to each other. The water then goes between the particles and is imbibed. There is no sharp dividing line between imbibition and solution, as substances may at first swell owing to the imbibition of water and the swelling may continue to such an extent that solution results.

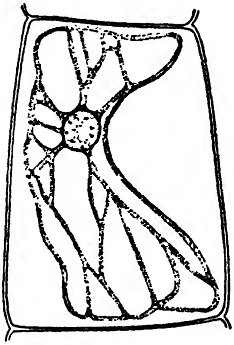

Fig. 76. A plasmolyzed cell from a hair of a squash shoot. (× 160)

TRANSPIRATION

Definition. Transpiration is the evaporation of water from plants, the water passing in the form of water vapor into the surrounding atmosphere.

Process. We have seen that water permeates the walls of the chlorenchyma cells, so that the surfaces of the walls surrounding the intercellular spaces are wet, and that this condition is necessary for the entrance of carbon dioxide into the cells. Since the wet surfaces of the cells are in contact with the air in the intercellular spaces, some of the water in the walls vaporizes and diffuses into this air, just as the water from wet clothes goes into the surrounding atmosphere while the clothes are drying. The accumulation of water vapor in the air in the intercellular spaces makes the water content of this air greater than that of the atmosphere surrounding the leaf, so that water vapor diffuses out through the stomata into the external atmosphere. The diffusion of water vapor from the intercellular spaces into the atmosphere tends to reduce the water content of the air in the intercellular spaces, and thus causes additional water to leave the cell walls and enter the intercellular spaces. The passage of water from the cell walls into the intercellular spaces, and then out through the stomata into the external atmosphere, is thus continuous as long as the cell walls are wet and the stomata are open. Since those conditions are necessary for the absorption of carbon dioxide for photosynthesis, transpiration is a constant concomitant of photosynthesis. In other words, the conditions that are necessary for photosynthesis make transpiration unavoidable. Transpiration is, strictly speaking, not a process of the plant itself but the result of the action of external conditions on the plant.

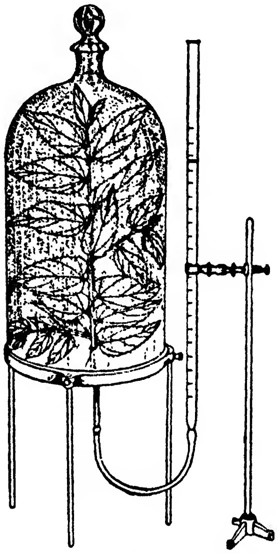

Fig. 77. Apparatus for demonstrating the loss of water by transpiration

Some water is lost from the epidermal cells. This is known as *cuticular transpiration.* The amount of water given off in this manner is, however, small as compared with that which diffuses out of the stomata.

Demonstration. That water is lost by transpiration can be demonstrated by the arrangement shown in Fig. 77. A branch is attached, by means of a rubber tube, to a burette containing water. The branch is then placed inside a bell jar, when some of the water that is transpired will condense on the sides of the jar. A potted plant may be used in place of the branch. This experiment can be checked by setting up a similar preparation with a dead, dry branch substituted for the living one. In this case no water will collect on the sides of the bell jar.

The amount of transpiration can be roughly determined in the manner shown in Fig. 78. A branch is attached, by means of a rubber tube, to a burette containing water. As transpiration continues, water is absorbed from the burette, the amount being shown by the change in the height of the water in the burette. This method is inaccurate, as it measures the amount of water absorbed rather than that given off, and, moreover, the transpiration of a severed branch is frequently very different from that of a branch on the plant. A more accurate method of measuring transpiration is by weighing. A potted plant can be used for this purpose. The pot and soil should be sealed in a waterproof covering so that water can evaporate only from the plant itself. The rate of transpiration can then be determined by weighing the preparation at definite intervals of time.

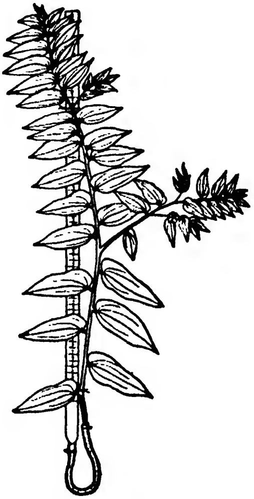

FIG. 78. Apparatus for measuring the amount of water absorbed by a transpiring branch

Harmful effects of transpiration. The most conspicuous effect of transpiration is the damage that results from excessive loss of water. If water is lost in transpiration faster than it is supplied from the roots, the leaves wilt; and if the excess of loss over supply continues, the plant will finally die. Even without actual wilting, the growth of plants may be greatly retarded by high rates of transpiration accompanied by a low moisture content of the soil. This condition is very evident in many crops during long dry seasons. Delicate plants, such as many ferns, cannot grow in dry places, because they lose more water by transpiration than they can absorb from the soil. The bareness of desert regions is due to excessive evaporation and the scarcity of water in the soil. If it were not for the high rate of evaporation, however, there would be enough water in the soil in many desert regions to support a fair growth of vegetation at all times.

Excessive loss of water is one of the greatest dangers to which many plants are exposed, and is one of the most frequent causes of the death of plants. The harmful effects of excessive transpiration account for the fact that the leaf is protected by a heavily cutinized epidermis and by stomata which close as the result of the loss of water.

Transpiration and temperature. The evaporation of water has the effect of cooling the object from which it evaporates, and so the transpiration of water from plants tends to reduce their temperature. This fact explains why living leaves remain relatively cool when exposed to intense sunlight, while dry objects, such as paper, become hot. If it were not for this cooling effect of evaporation, leaves would be overheated on hot, sunny days. Animals, like plants, may be benefited by the cooling effect of evaporation. The reason why we feel cool when in front of an electric fan is that the wind increases the rate of evaporation of water from our bodies.

One danger of high leaf-temperature is illustrated by the injury known as scalding. On hot days this injury sometimes results from the heating effect of intense sunlight following a shower which has left a high percentage of moisture in the air. The humidity lowers the rate of transpiration, with the result that the leaf becomes overheated. The injurious effects of high temperatures are, however, not confined to such conspicuous injuries as the one just mentioned. Many physiological processes, including growth, are affected by excessive heat.

Transpiration and mineral matter. When the chlorenchyma cells of the leaf lose water through transpiration, the osmotic pressure in them is increased. This increase in osmotic pressure results in the diffusion of water from the xylem of the veins to the chlorenchyma, to replace the water lost by transpiration. The xylem is continuous from the leaf through the stem to those parts of the roots where water is absorbed. In the xylem water moves not by diffusion, but as a steady stream through long tubes composed of dead cells. This stream of water carries the dissolved mineral matter along with it to the veins of the leaf, where both the water and the mineral matter can diffuse into the cells of the chlorenchyma. The movement of salts from the veins into the chlorenchyma, being by diffusion, is independent of the passage of the water but dependent on the relative concentration of the particular kind of matter in the chlorenchyma cells and in the veins. The reason why the kinds of mineral matter that are used in the leaves continue to diffuse into the chlorenchyma is that in their assimilation they are combined with other compounds and are thus changed to different substances. When a given substance combines with another to form a new compound, the concentration of the original substance is decreased. Owing to this fact a substance which is in solution in the xylem of the veins will continue to diffuse into the chlorenchyma as long as it is used by being combined with some other compound. The importance of transpiration in the passage of mineral matter into the leaves is that transpiration causes a stream of water to pass through the xylem and that this water carries dissolved material into the veins, where it can diffuse into the chlorenchyma.

The rate of the movement of mineral matter into the leaves is not necessarily proportional to the rate of transpiration, as the movement of dissolved material from the xylem into the chlorenchyma is by diffusion and depends on the relative concentration of the particular dissolved material in the two tissues, while the entrance of dissolved substances into the root is also by diffusion and depends on the relative concentration in the soil and root. Actual experiments indicate that under ordinary conditions there is little relation between rates of transpiration and the amount of mineral matter in plants. It would appear that plants are frequently subjected to higher rates of transpiration than are necessary for the movement of sufficient dissolved material through the xylem.

While some transpiration would appear to be beneficial, particularly to tall plants, because it accelerates the movement of dissolved material from the roots to the leaves, there are at least many small plants for whose development it would seem to be unnecessary, as is shown by the fact that they will grow in an atmosphere kept as nearly saturated with water as is possible even under experimental conditions. In the absence of transpiration the movement of dissolved materials can take place through the plant slowly by means of diffusion.

Factors influencing transpiration. The rate of transpiration varies greatly with changes in the environment. The factors that affect transpiration are the same as those that influence the rate of evaporation in general.

The effects of light, heat, wind, and humidity on ordinary evaporation are matters of common knowledge. We know that if we put a wet handkerchief in a warm place it will dry much more rapidly than it would in a cold place. The drying of the handkerchief is, of course, simply the evaporation of water from the handkerchief. We know also that wet clothes will dry more rapidly in sunlight than in a dark or shaded place, and, other conditions being equal, more rapidly on a windy day than on a still day. Likewise they will dry more rapidly on a dry day than on a very moist one.

Transpiration varies with the temperature, because water vaporizes more rapidly at high temperatures than at low temperatures, and because warm air absorbs more moisture than cool air does. Light increases transpiration, owing to the heat produced by the light. Wind increases transpiration in two ways: diffusion of water vapor from the stomata tends to saturate the atmosphere around the leaves, but wind removes this moist air and replaces it by drier air; wind also, by causing the leaves to shake and bend, increases the movement of gases in the intercellular spaces. Again, the rate of transpiration is greatly influenced by the humidity of the air, that is, the amount of water vapor in the air. Dry air not only absorbs more moisture than wet air does but absorbs it more rapidly. Therefore the rate of transpiration decreases with rising humidity.

Control of transpiration. The rate of transpiration is greatly influenced not only by external conditions but also by the plants themselves. This is brought about in two general ways: by *permanent morphological changes* which restrict or accelerate the rate of transpiration, and by *physiological changes* which control the rate temporarily.

Restriction of transpiration. Among the structural modifications which may influence the rate of transpiration are the number and size of the leaves, the thickness of the leaves, the compactness of the chlorenchyma, the number and arrangement of the stomata, the thickness and cutinization of the epidermal walls, and the development of trichomes (outgrowths from the epidermal cells).

Number and size of leaves. Other things being equal, the amount of water transpired by a plant will tend to vary with the number and size of its leaves, as the more surface the plant has for transpiration the more water it can transpire. It is not surprising, therefore, to find that most plants growing in moist regions have a large number of fair-sized leaves. When the leaves are few in number they are usually large. On the other hand, plants growing in an arid region will usually have few and small leaves, so that the rate of transpiration is restricted by a reduction in the transpiring surface.

Gardeners, when transplanting large plants, very commonly reduce the number of leaves, to restrict transpiration. In removing a plant from the soil the parts of the roots which absorb water are destroyed to a very considerable extent. The plant can therefore absorb less water and so has less water for transpiration. In order to balance this effect it is a usual practice to remove a considerable portion of its leaves.

Thickness of leaves. If the leaves of a plant are thick, they will have a smaller outside area per unit of volume than they would have if they were thin. Therefore thin leaves will transpire more per unit of volume than will thick leaves. In keeping with this fact we find that plants growing in very moist places usually have thin leaves, while those which are exposed to dry conditions have thicker leaves.

Compactness of chlorenchyma. If the cells of chlorenchyma are arranged close together, there will be a less free circulation of gases inside the leaf than there would be if the cells were loosely arranged, with large intercellular spaces; consequently, the more the spongy chlorenchyma is replaced by palisade the more the rate of transpiration will be restricted. The relative development of the palisade and the spongy chlorenchyma cells varies greatly under different environmental conditions. In very moist places, as in damp, shaded ravines, the spongy chlorenchyma usually occupies a larger portion of the leaf than does the palisade, and not infrequently the palisade disappears entirely (Fig. 897). In dry regions the reverse is the case. Here the spongy chlorenchyma is usually less conspicuous than the palisade. The leaves may have a thin layer of spongy chlorenchyma near the lower epidermis; or the layer of spongy chlorenchyma may be between two layers of palisade (Fig. 79), one below the upper epidermis and the other just above the lower epidermis; or, again, the spongy chlorenchyma may be entirely replaced by palisade chlorenchyma. Note the difference in the development of the palisade and the spongy chlorenchyma as shown in Fig. 48 and also in Figs. 26 and 28. The relative development of the palisade and the spongy chlorenchyma may be suited not only to various rates of evaporation but also to various intensities of light. In damp ravines the light is usually of low intensity, and in such situations not much light would be likely to pass through thick layers of tissue. On the other hand, in dry regions the

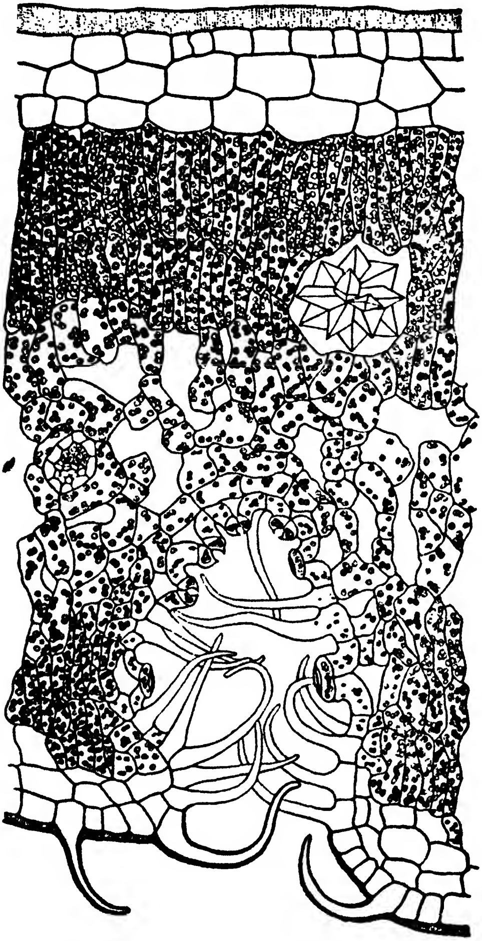

Fig. 79. Cross section of a leaf of oleander (*Nerium*) with upper and lower palisade, three-layered upper epidermis, and stomata in a pit protected by trichomes. (× 285)

atmosphere is likely to be clear and the intensity of light to be very great; under such conditions light sufficient for photosynthesis would penetrate through a much thicker layer of tissue than would be the case with plants exposed to lower intensities of light.

Number and arrangement of stomata. The rate of transpiration will naturally vary with the number of stomata. Plants growing in moist situations are likely to have more stomata per unit of area than those in dry regions. Some plants which are natives of arid localities have stomata that are sunk in pits (Figs. 79, 80), while some which are found in moist regions have their stomata raised above the general level of the epidermis. More water will naturally be transpired through exposed than through protected stomata.

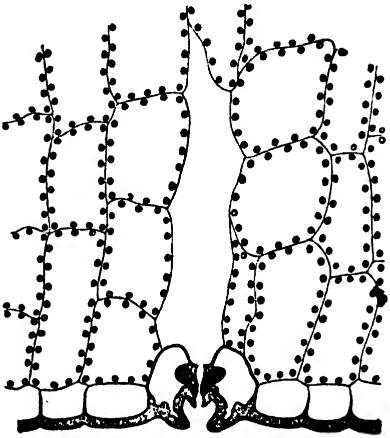

FIG. 80. Cross section of a portion of a leaf of a century plant (*Agave cantula*), showing a sunken stoma. (× 170)

Thickness and cutinization of epidermal walls. The chief function of the epidermis is to restrict the amount of transpiration by means of its thick and cutinized outer walls. The amount of transpiration will, of course, decrease as the thickness and the cutinization of the wall increase. Plants growing in dry situations have thicker epidermal walls than those in moist regions. Even on the same plant, leaves exposed to the sun have thicker epidermal walls than those in the shade (Fig. 48). Xerophytic plants may have not only thick epidermal walls but also an epidermis composed of more than one layer of cells (Fig. 79).

Development of trichomes. Many leaves have hairs on their surfaces. These hairs are outgrowths from the epidermal cells and are frequently dead. If such dead hairs are numerous and close together, they will have a tendency to decrease the rate of transpiration, as they tend to minimize the movement of air near the stomata.

Hereditary and acquired modifications of structure. The changes in structure which restrict or accelerate the rate of transpiration are of two general classes: those changes which are characteristic of a species and are hereditary, and those which are acquired by individual plants or leaves in response to the condition under which they are grown.

Acquired modifications. Even on the same plant some leaves may be more exposed than others to the effects of evaporation, as they are not all equally exposed to the action of sun and wind. We usually find that on the same plant the leaves that grow in the sun are thicker and have their chlorenchyma more compact and their epidermal walls thicker than the leaves that grow in the shade (Fig. 48). These differences are due to the response of the individual leaves to their environment. A practical application is made of this fact in growing tobacco under shade in order to obtain large, thin, and pliable leaves to be used as cigar wrappers. While leaves respond, to a certain degree, in the ways mentioned above, the possible extent of such response is limited.

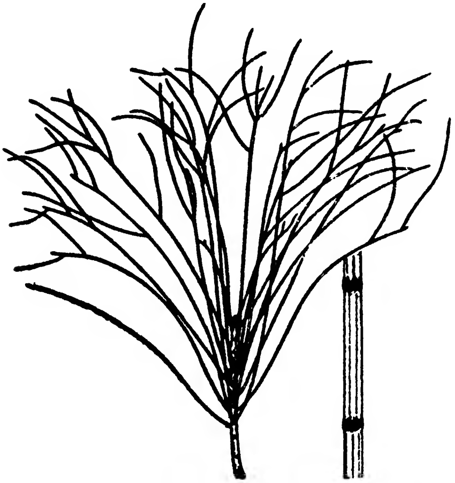

Fig. 81. Branches of *Casuarina* with scalelike leaves. (× ⅓)

The small figure on the right shows a piece of a branch with whorls of scalelike leaves at the nodes. See Fig. 124

Hereditary modifications. Besides the response of individual leaves and plants to different environments there are hereditary modifications of leaf structure which may be more pronounced and which fit plants for different environmental conditions. On many desert plants the leaves are reduced to rudimentary structures or are modified into spines (Figs. 81, 82, 277). No matter under what conditions these plants may be grown, they will not

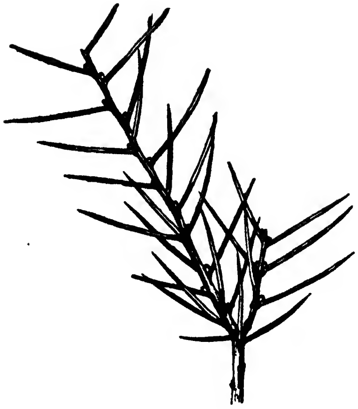

FIG. 82. A branch of an Australian desert plant, *Hakea*, with the leaves modified as spines. (× ½)

develop large leaves. Likewise, delicate ferns will not develop leaves which can resist the high rates of evaporation that occur in desert regions. Plants which are natives of the desert and have very small leaves may, if grown in moist regions, develop somewhat larger leaves, but they will never develop leaves of any great size. While environment may have a marked influence on leaves, heredity is in general more important than environment in determining their size.

Fig. 83, which represents a cross section of a leaf, shows an interesting hereditary modification suited to a particular kind of environment. The thick, water-storing epidermis helps the plant to endure short periods of comparative dryness, while the single layer of chloroplasts indicates a shady habitat.

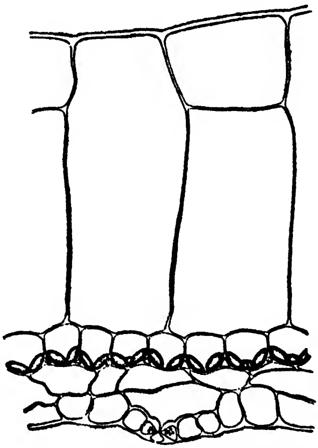

FIG. 83. Cross section of a leaf of *Peperomia pellucida*, a tropical plant that thrives on shady stone walls

Note water-storing upper epidermis and single layer of cells with chloroplasts

Effect of evaporation on distribution of plants. In nature we find that plants of desert, fairly moist, and very moist regions are all specially fitted for the conditions under which they grow, and that the structural modifications which fit them for their native localities are fixed by heredity to such an extent that usually they will not thrive under conditions that are very different from those of their natural habitat. The rate of evaporation is one of the most important environmental factors for which plants are fitted, and the rate of evaporation determines, to a considerable extent, the kinds of plants which grow naturally or can be cultivated profitably on any given area. If the soil is sufficiently irrigated, many crop and garden plants which are suited to fairly moist conditions can be grown successfully in regions that are naturally dry; but there are many plants which cannot withstand the very high rates of evaporation prevailing in arid regions, no matter how much water is in the soil. Many desert plants can stand much more moist conditions than those under which they normally occur, and can be successfully cultivated in moist regions; but when left to themselves they are not able to compete with the vigorous plants of moist areas.

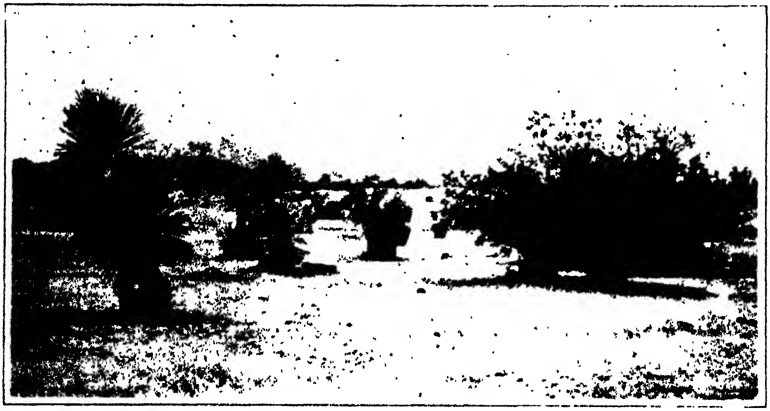

Fig. 84. Desert region in Arizona with *Yucca alata* to the left and *Prosopis velutina* to the right

High rates of evaporation, accompanied by a small percentage of water in the soil, result in an open growth of small plants (Figs. 84, 276–278); low rates of evaporation and abundant moisture in the soil, other conditions being favorable, bring about a dense forest of tall trees (Figs. 6, 250).

Regulation of transpiration. The rate of transpiration is regulated more or less temporarily in a number of different ways. The most important of these are by deciduous leaves, by the drying of the walls of the chlorenchyma, and by the opening and closing of stomata. There are also some other means, such as the rolling and folding of leaves, which reduce the transpiring surface.

Deciduous leaves. Broad-leaved trees which grow in regions that have either a very cold or a very dry season usually shed all their leaves during such periods of cold or of drought. Of course the shedding of the leaves greatly restricts transpiration.

When the weather is very cold, plant roots can absorb little water from the soil, while if the leaves were exposed to the air they would continue to transpire. This is one of the reasons why broad-leaved trees in the colder parts of the temperate zone shed their leaves at about the beginning of the cold season (Fig. 258).

A very similar result ensues when trees are subjected to a long, pronounced dry season. At such times both the soil and the air will usually contain comparatively little moisture, with the result that if trees had an extensive leaf area, their roots could not absorb enough water to supply that which would be lost by transpiration. The shedding of leaves by plants of the temperate zone during the autumn, and by tropical plants which grow in regions with a pronounced dry season, is therefore the result of very similar circumstances. In tropical regions where there is no pronounced dry season, plants retain their leaves throughout the year.

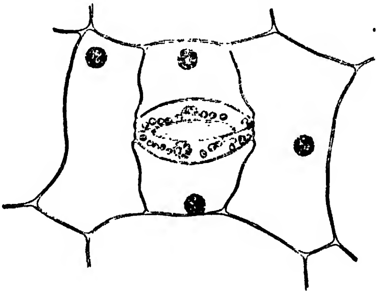

FIG. 85. Surface view of a stoma of Wandering Jew (*Zebrina pendula*). (× 145)

The drying of chlorenchyma walls. On hot, dry, sunny days the leaves of plants may lose more water than the roots can absorb. The result of this is that the cells, and also the cell walls, then contain less water than when transpiration is less rapid. Very wet substances naturally lose more water than drier ones; and so, as the cell walls become drier, less water diffuses from them into the intercellular spaces. The rate of transpiration is thus automatically lowered.

The opening and closing of stomata. A stoma is an opening between two sausage-shaped cells called *guard cells*. Fig. 85 shows a view of a partly open stoma, and Fig. 86 a cross section through a closed stoma and surrounding cells. The guard cells are constructed in such a way that they can move so as to open and close the stoma. Stomata are usually closed at night and open in the day; but when the rate of evaporation is rapid, they also close during the day. When the guard cells are turgid the stomata are open, while as the guard cells lose their turgidity the stomata close.

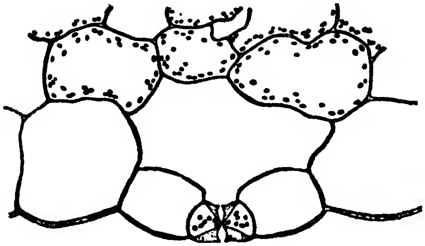

Fig. 86. Cross section of a stoma and surrounding cells of Wandering Jew (*Zebrina pendula*). (× 130)

Mechanism of opening and closing of stomata. To understand how changes in the turgidity of the guard cells cause the opening and closing of the stomata it will be necessary to study the structure of the guard cells. There are a number of types of guard cells, but for simplicity we may consider only what is probably the most widely distributed one. A transverse section through a guard cell (Fig. 87) shows that the wall which is farthest from the stomatal pore (dorsal wall) is very thin, while that which is next to the pore (ventral wall) is much thicker. When the guard cells become turgid their walls naturally tend to stretch; but the ventral walls, owing to their great thickness, stretch much less than do the dorsal walls. The result is that the cells become bent, with the concave side toward the pore. This is the principal cause of the opening of stomata. When the guard cells lose their turgidity they straighten out and come together, thus closing the stomata. This type of bending can be illustrated by means of a rubber tube or an elongated toy balloon, to one side of which adhesive tape has been attached. When the tube is inflated it will bend, the side to which the adhesive tape has been applied being the concave side (Fig. 88).

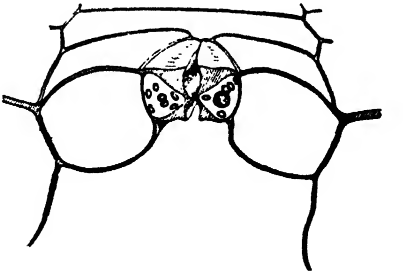

Fig. 87. Combined cross section and surface view of a stoma

The ventral wall is not uniformly thickened. In the center, as seen in cross section, it is thin. Away from the center it is greatly thickened, and along the edges it projects into the stomatal pore. The central part of the wall also bulges into the pore. The stomatal pore is thus not of uniform diameter, but consists of two more or less enclosed chambers which are connected by means of a narrow passage. The fact that the ventral wall is composed of two thickened ridges connected by a thin strip has distinct advantages. These ridges are so thick that they offer resistance to any tendency to stretch them, so that when the cell becomes turgid and the thin dorsal wall is stretched, the thin part of the ventral wall bends and there is a tendency for it to be drawn away from the center of the stomatal opening, thus enlarging that opening. This type of movement can be imitated roughly by means of two boards fastened together at one end by a piece of leather to represent the thin part of the ventral wall, and at the other end by a rubber band to represent the dorsal wall (Fig. 89). If the rubber band is stretched, it will be seen that the other ends of the boards are drawn to it. When the guard cell loses its turgidity, the dorsal wall contracts and the thin part of the ventral wall bulges out, and it is this part which closes the stomatal passage. It is an advantage to have the passage closed by the thin part of the ventral walls (Fig. 87), as thin walls can be pressed much closer together than could thick, rigid ones.

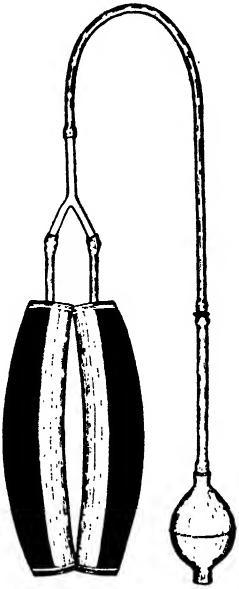

FIG. 88. Apparatus to imitate the opening and closing of a stoma

The two large rubber tubes with adhesive tape on the adjacent sides are inflated by means of the rubber bulb

Factors affecting opening and closing of stomata. The guard cells contain well-developed chloroplasts, while these are usually not present in the other cells of the epidermis, except in some plants that grow in moist, shady situations. During the day the contents of the guard cells have a high osmotic pressure. Consequently when the surrounding cells are well supplied with water the guard cells draw water from them and become turgid, and the stomata open. If, however, the plant loses more water from its leaves than is absorbed by its roots, the water content of the cells of the leaf, including the guard cells, is lowered, and the guard cells become less and less turgid. As this process continues the stomata close. The rate of transpiration is regulated to a considerable extent by the opening and closing of stomata. The closing of stomata does not, however, entirely stop transpiration, as a small amount of transpiration takes place through the cuticle of the epidermal cells.

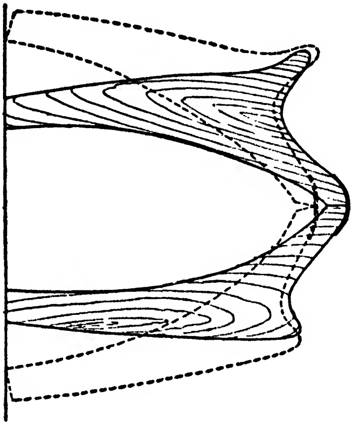
Fig. 89. Arrangement to imitate the bending of the ventral walls of a stoma

Daily march of transpiration. The rate of transpiration is dependent to a considerable extent on the rate of evaporation. Therefore we shall consider first the variations in the rate of evaporation at different times during the day and night. During the night the rate of evaporation is usually very low, as at this time the air is much colder than during the day and the accelerating influence of sunlight is absent. The air is also much more nearly saturated with water during the night than during the day; for cold air can hold less water than warm air, and thus, although there may be the same amount of water in the air during the day and during the night, the air becomes more and more saturated as it cools during the night. We see the result of this phenomenon in the formation of dew by the condensation of water from the air. This condensation takes place at night because the air is more nearly saturated at that time than during the day. The increase in the saturation during the night has a great retarding effect on the rate of evaporation. With the coming of daylight the rate of evaporation increases, owing to light, greater heat, and the fact that the air becomes less saturated with water as it gets warmer. This increase in the rate of evaporation usually continues on bright days until some time in the afternoon. As the sun goes down the rate decreases, and the decrease continues until the low night rate is reached.

If the rate of evaporation is comparatively low during the day, the rate of transpiration may follow that of evaporation rather closely. But when the rate of evaporation during the day increases to a point where transpiration is excessive, the rate of transpiration is restricted by the movements of the guard cells and the drying of chlorenchyma walls. Thus it frequently happens that while the rate of evaporation continues to increase until some time in the afternoon, the highest rate of transpiration is reached in the morning. At night the rate of transpiration is low, owing to the very low rate of evaporation and to the closing of the stomata.

Water content of the leaf. Many leaves contain from 80 to 90 per cent of water. When, on a dry day, a plant loses more water than it absorbs, the water content of the leaves naturally diminishes; thus it very frequently happens that leaves contain less water during the middle of the day than during the night. In many plants the loss of water goes so far on dry days as to cause an actual wilting of the leaf. Not only leaves but other parts of plants frequently contain less water during the day than at night. It is for this reason that vegetables have a crisper and fresher appearance when picked early in the morning than when gathered later in the day.

The relation of moisture to number and size of leaves has been treated in a previous paragraph.

CHAPTER VII

SPECIALIZED LEAVES

The principal function of ordinary foliage leaves is photosynthesis. Besides the primary function of foliage leaves they also perform such functions as respiration and growth, which are common to all living parts of plants. In addition we find that many leaves are specially modified to perform functions which are not usually the principal ones of leaves, or are modified to carry on the principal function in an unusual manner. Such leaves may be called specialized leaves. As examples of leaves which perform the primary function of leaves in an unusual manner we may mention such leaves as those of oranges and grapefruits, where the petiole has a bladelike structure and is especially fitted for photosynthesis (Fig. 90), and the stipules of the garden pea (*Pisum sativum*), which are bladelike and have the functions of a blade (Fig. 94). The special functions for which some leaves are particularly suited may be grouped under six headings: *support* (stem function), *absorption* (root function), *attraction of insects* (floral function), *reproduction* (seed function), *storage*, and *protection*. These functions may be subsidiary to the ordinary functions of leaves, or be more important, or even replace the usual functions.

Support (stem function). The primary function of stems is to support the aerial parts of the plants. This function is performed by four special types of leaves: tendrils, which may be modified whole leaves or parts of leaves; leaves with hooks; leaves with floats; and leaves that have supporting leaf bases.

Supporting leaf bases. The leaf bases of the banana and other similar plants are greatly elongated and grow so close together as to produce a structure which has an appearance very much like that of an ordinary trunk, and which supports the leaf blades and the fruit in much the same way as does a trunk (Fig. 91). The main stem is thick and short, with a convex top to which the

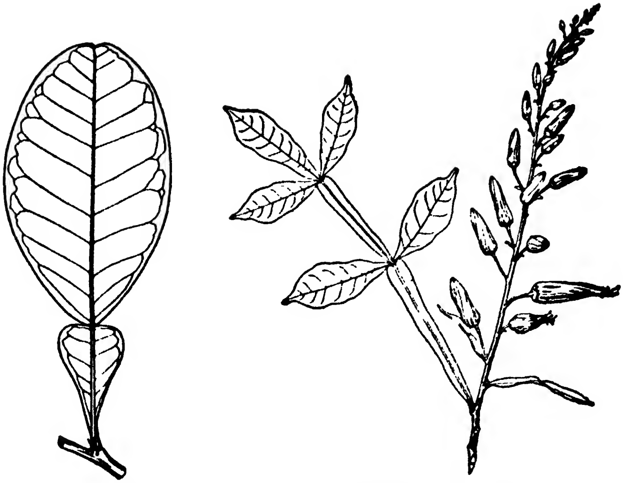

FIG. 90. Leaves showing bladelike petioles

Left, Philippine grapefruit (*Citrus decumana*) (× $\frac{1}{3}$). Right, *Quassia amara* (× $\frac{1}{4}$)

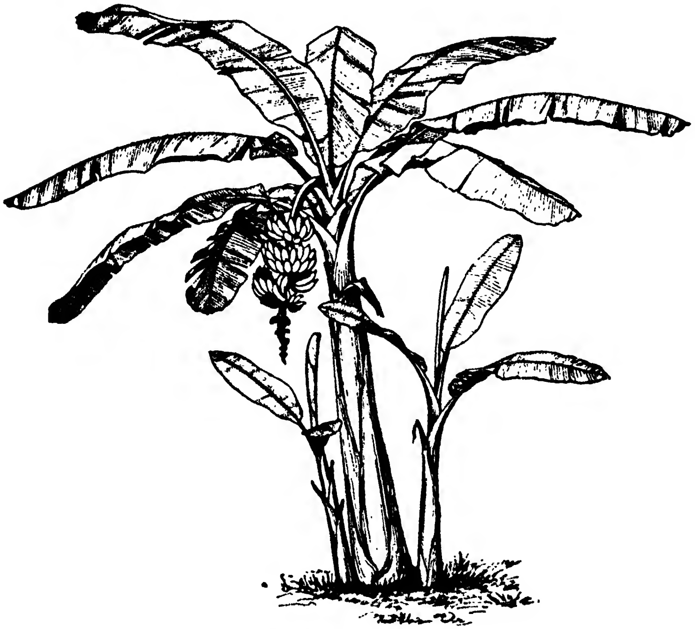

FIG. 91. Banana plant. (× $\frac{1}{42}$)

leaf bases are attached. The slender fruiting stalk pushes up in the center of the elongated leaf bases and is supported by them (Fig. 92).

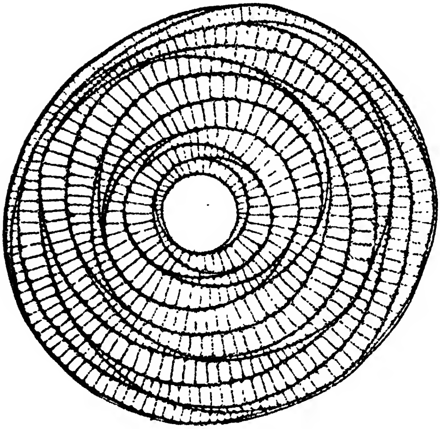

Fig. 92. Cross section of the false trunk of the banana plant, showing small flowering stalk surrounded by leaf bases. (× ½)

In grasses the younger part of the stem has a soft growing region just above the attachment of each leaf. This growing region is so soft and weak that it could not, by itself, support the part of the plant above it. The leaf base has the form of a long, slender tube which surrounds and supports the stem and enables it to bear its load (Fig. 93).

Tendrils. The climbing plants have slender stems which do not possess sufficient strength to hold themselves erect. Such plants catch on to other objects, particularly other plants, and thus make use of the strength of these other objects to support them. This enables them to grow up into the sunlight without expending the material which would be necessary to build a strong trunk. Tendrils are one of the means by which plants hold on to other objects. Tendrils are long, slender structures which curl around objects with which they come in contact. They are frequently, but by no means always, modi-

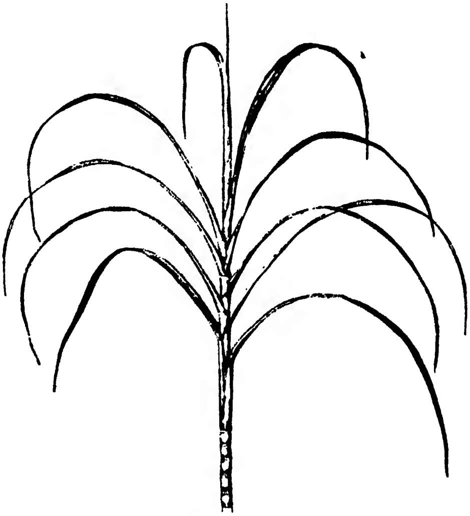

Fig. 93. Tip of stalk of sugar cane. (× $\frac{1}{30}$)

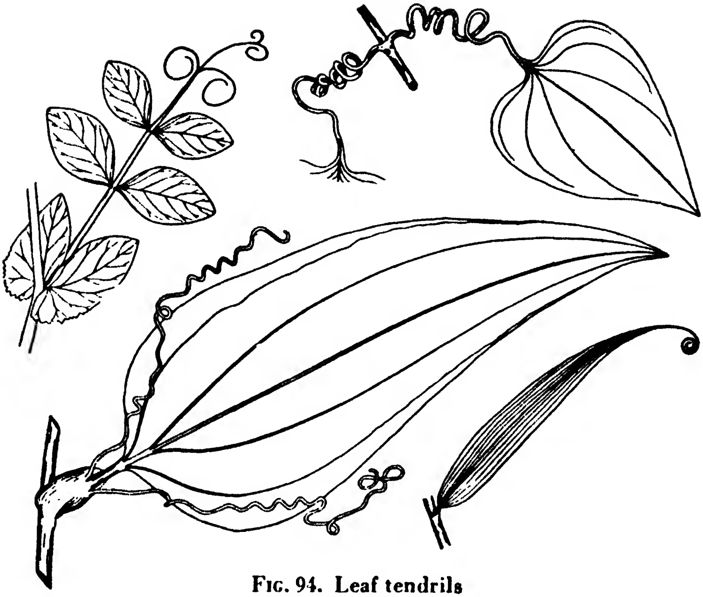

FIG. 94. Leaf tendrils

Upper left, *Pisum sativum*; upper right, *Clematis smilacifolia*; lower left, *Smilax leucophylla*; lower right, *Flagellaria indica*. (× $\frac{1}{3}$)

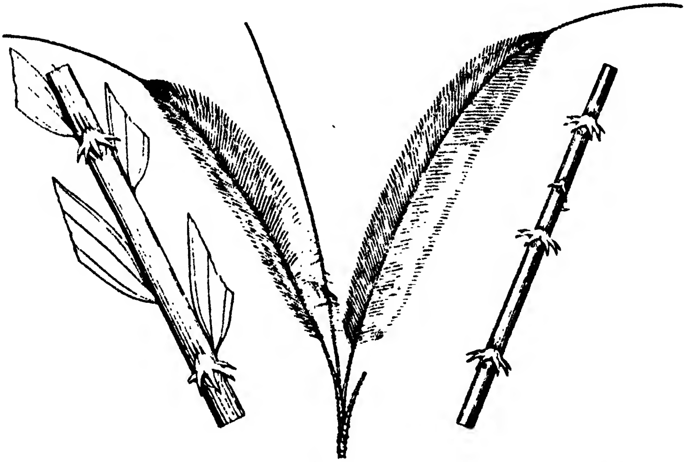

FIG. 95. Tip of a stem of a rattan palm (*Calamus*). (× $\frac{1}{38}$)

Left, back of rachis; right, back of extension of rachis

fied leaves. Any part of a leaf may be modified in this manner. Tendrils may be modified whole leaves, petioles (Fig. 94), leaflets as in the garden pea (*Pisum sativum*) (Fig. 94), tips of leaves (Fig. 94), or stipules (Fig. 94).

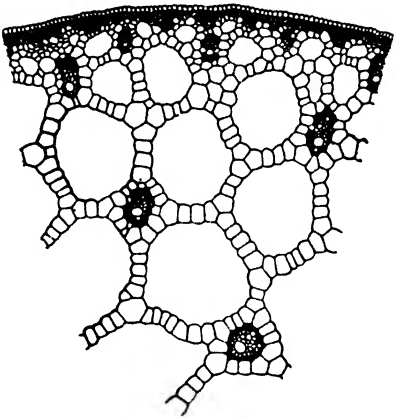

Fig. 96. Large air spaces in bulbous petiole of water hyacinth (*Eichhornia crassipes*). (× 30)

Hooks. Some climbing plants have leaves with hooks which enable them to hold on to other objects. Excellent examples are afforded by the climbing palms known as rattans (Fig. 251). These have large feathery leaves with numerous curved sharp-pointed hooks (Fig. 95) which catch on to objects with which they come in contact and thus support the stem and enable the plant to climb. Some climbing plants have stipular hooks which serve the same purpose. In the tomato the stiff backward-slanting rachis of the leaf acts as a hook.

Floats. The floating plants develop very loose tissue with large air spaces (Fig. 96). Such tissue enables the plant to float on the surface of the water. The bulbous petiole of the water hyacinth is occupied largely by air spaces and presents a striking case of the development of floating tissue (Figs. 96, 97). Similar tissue is found in the blades of floating leaves (Fig. 5).

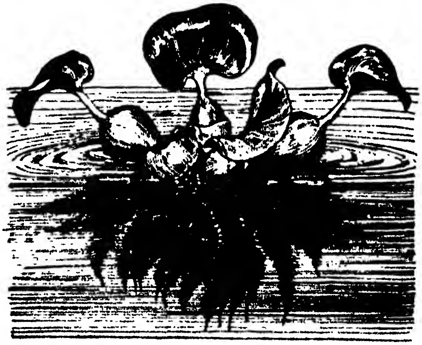

Fig. 97. Water hyacinth (*Eichhornia crassipes*) with petioles modified as floats. (× ⅓)

The air spaces in plants serve for aeration, that is, the exchange of gases between the cells and the external atmosphere. Fre-

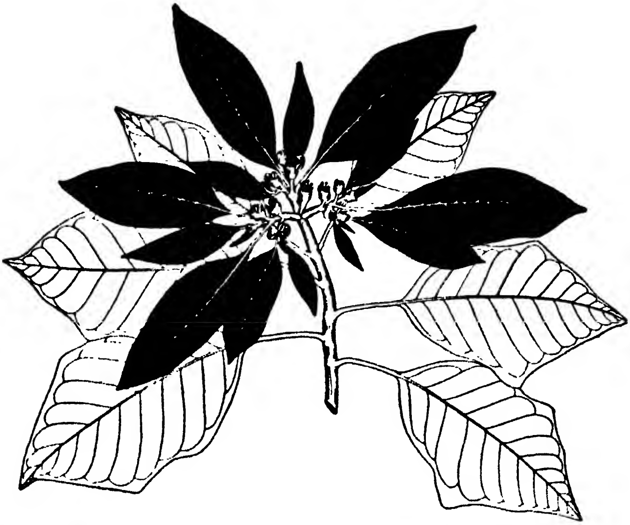

FIG. 98. Branch of poinsettia (*Euphorbia pulcherrima*). (× ¼)

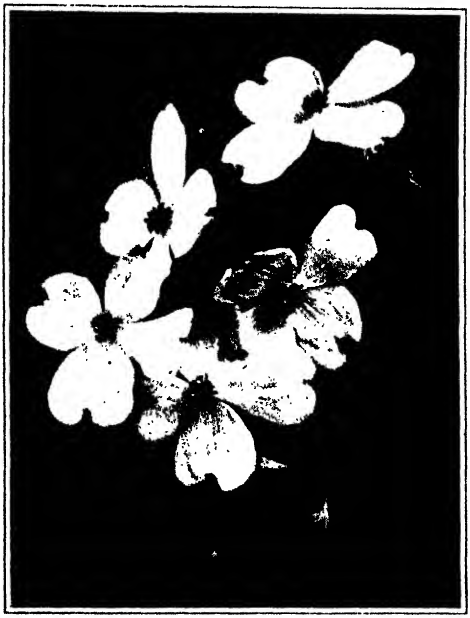

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FIG. 99. Dogwood (*Cornus florida*)

The conspicuous petal-like structures are modified leaves which surround small flowers quently the large air spaces in aquatic plants are primarily useful for this function, as is particularly true of the large air tubes which traverse the petioles of water lilies (Fig. 74) and by which the oxygen set free in the leaves by photosynthesis is allowed to diffuse to the roots.

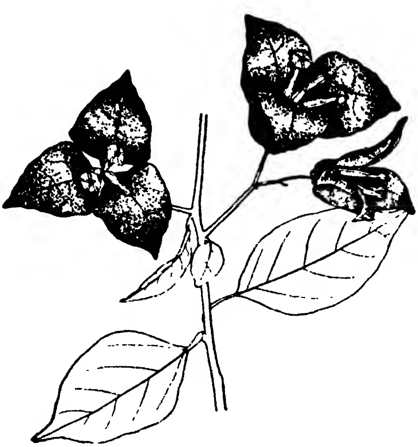

FIG. 100. Bright-colored bracts surrounding the small flowers of *Bougainvillea spectabilis*. (× ½)

Absorption (root function). One of the chief functions of roots is to absorb water as well as compounds of nitrogen and other elements which plants usually obtain from the soil. Most leaves are incapable, under ordinary circumstances, of absorbing these substances, but many plants have leaves which are especially fitted for this function. Such leaves fall rather naturally into two general classes: those especially fitted for absorbing water and the things which are ordinarily dissolved in it, and those that catch insects or other small animals and obtain nutrient substances in this manner.

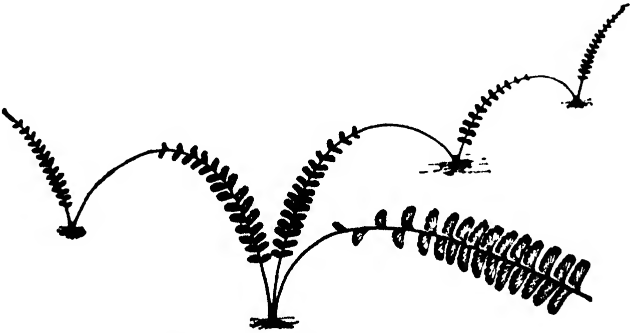

FIG. 101. A walking fern (*Adiantum caudatum*). (× ¼)

Water-absorbing leaves. The leaves of submerged plants are not ordinarily exposed to evaporation and do not have cutinized epidermal walls. They are surrounded by water in which mineral matter is dissolved, and so can absorb these substances directly.

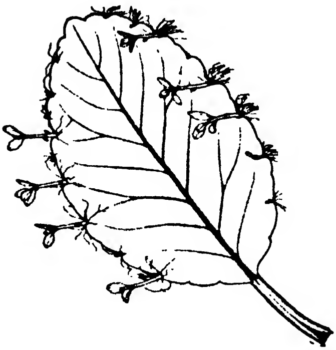

Fig. 102. Leaf of life plant (*Bryophyllum pinnatum*) producing small plants. (× ⅓)

Many plants growing in dry situations have leaves that are provided with absorbing hairs. These may be of great advantage to a plant by enabling it to absorb water from light rains which do not wet the soil, or even from dew. They are of considerable use to plants growing in situations where for long periods there may be dew every night but no rain. Dew is condensed on, and absorbed by, these hairs. Some plants have leaves which are especially fitted for collecting and absorbing water. The bromeliads (plants of the pineapple family) furnish excellent examples of absorbing hairs (Fig. 252).

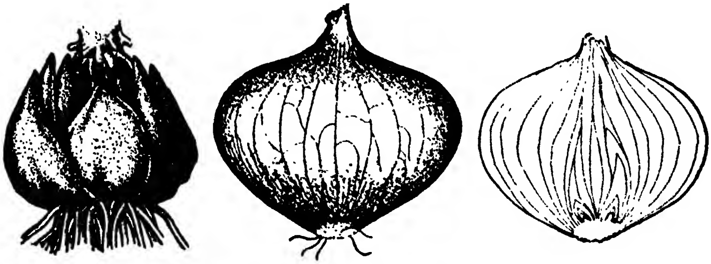

Fig. 103. Bulbs of lily and onion

Left, lily; center, exterior view of onion bulb; right, section of onion bulb

Carnivorous leaves. There are several different types of leaves which catch insects and other small animals from which the plant obtains nitrogenous materials. These have been discussed in the chapter on assimilation.

Attraction of insects (floral function). The principal function of white or brightly colored petals is to attract insects or other animals which pollinate the flowers. As we shall see later, the petals are modified leaves. Aside from petals there are other types of leaves which serve to attract insects. In some cases the flowers are small, and the function of attracting insects is performed by large white or brightly colored leaves. These leaves may have the shape of ordinary foliage leaves and differ from them largely in being white or brightly colored, as in the case of the poinsettia (Fig. 98). In other cases the leaves (bracts) have a shape very different from that of foliage leaves (Figs. 99, 100). In many cases it is not the flowers themselves but the bracts that are showy.

Fig. 104. A staghorn fern (*Platycerium biforme*) growing on a coconut trunk. (× ½)

Reproduction (seed function). Many plants can be propagated by means of leaf cuttings; this form of propagation is commonly practiced in the case of begonias. Some plants in their wild state reproduce regularly by means of leaves. Striking examples are afforded by the so-called walking ferns and by *Bryophyllum.* The walking ferns have long leaves the tips of which reach the ground, strike root, and grow into new plants (Fig. 101). The leaves of *Bryophyllum* have small notches in their margins. When these leaves fall or are removed from the parent plant, small plantlets grow from the notches (Fig. 102). These plantlets send roots into the soil and grow into large plants.

Storage. Leaves that are specialized for storage can be divided into three general classes: leaves with special water-storage tissue, those with special food-storage tissue, and those which form pockets for collecting materials out of which the roots absorb such substances as are ordinarily obtained from the soil.

Water storage. Some plants which grow in very dry regions have leaves that are greatly thickened by water-storage tissue. Such tissue is very prominent in the leaves of the century plant (*Agave* spp.). Special water-storage tissue is not confined to leaves that are greatly thickened, but also occurs in some which have the appearance of ordinary foliage leaves (Figs. 79, 83). This is true of such plants as the India rubber tree familiar as a house plant (*Ficus elastica*).

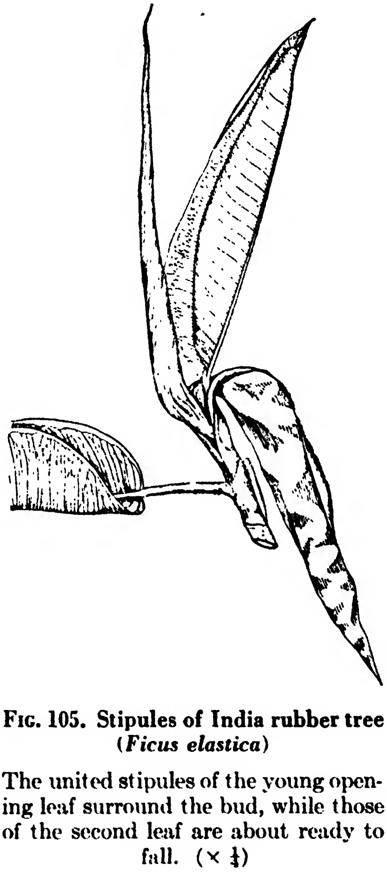

Fig. 105. Stipules of India rubber tree (*Ficus elastica*)

The united stipules of the young opening leaf surround the bud, while those of the second leaf are about ready to fall. (× ½)

Food storage. Fleshy bulbs are composed largely of thickened leaf bases, as in the onion (Fig. 103), or of whole leaves, as in lilies. In both cases the leafy part of the bulb serves for the storage of food.

Pocket leaves. A considerable number of epiphytic tropical plants have the lower portion of their leaves, or special leaves, modified into pocket-like structures, in which leaves, dust, and other debris collect. The roots grow into this debris and absorb materials from it (Fig. 255). The staghorn fern is a well-known example (Fig. 104). This plant has two types of leaves: ordinary foliage leaves which hang down, and collecting leaves which surround the mass of roots.

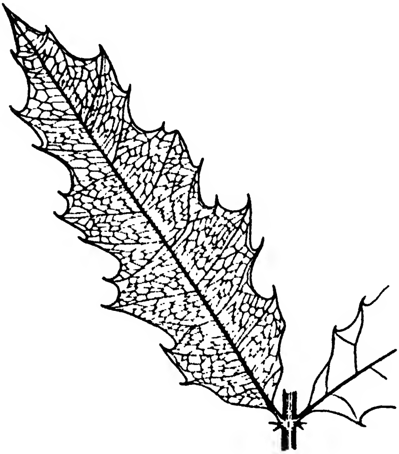
FIG. 106. Marginal and stipular spines of the simple leaf of *Acanthus ilicifolius*. (× ½)

Water collects in the cups formed by the overlapping lower portions of the leaves of some bromeliads and is absorbed by the leaves (Fig. 252).

Protection. At the tip of a growing stem there is a soft growing region which is surrounded and protected by the young leaves. This protection may be afforded by whole leaves or by stipules (Figs. 15, 105). Aside from this protective function, many leaves are specially modified for protecting the plant. The different kinds of leaves which have this special function may be divided into three classes: spiny leaves, motile leaves, and bud scales.

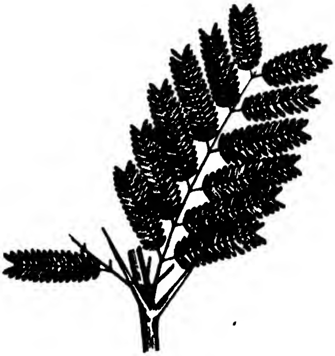
FIG. 107. Stipular spines of the bipinnate leaf of cassie flower (*Acacia farnesiana*). (× ½)

Spiny leaves. A large number of animals feed directly on plants. In some cases this is of advantage to the plants, as when birds eat the fruits of a plant and scatter the seeds; but the feeding of animals on the foliage or stems can be regarded only as harmful to the

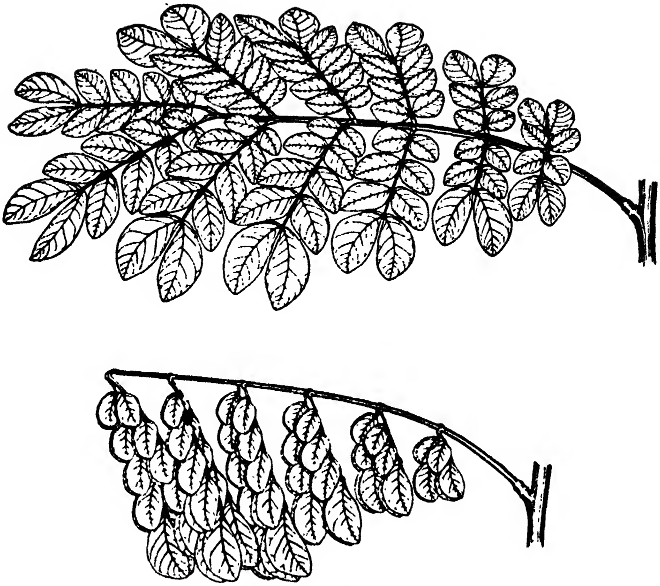

Fig. 108. Day and night positions of a leaf of a rain tree (*Enterolobium saman*). (× ⅓)

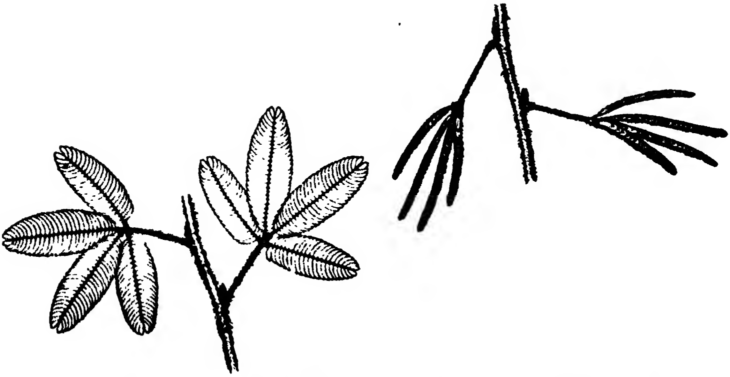

Fig. 109. Leaves of sensitive plant (*Mimosa pudica*) before and after stimulation. (× ⅓)

plants. Many plants are protected from animals, to a greater or less degree, by the development of spines (Fig. 106). On the other hand, many spiny plants are eaten by browsing animals. Spines may be stem or root structures, but very frequently they are modified leaves. Whole leaves that are modified as spines (Fig. 82) may or may not serve for photosynthesis. The spines of the cacti (Fig. 277) are believed to be modified leaves. In some cases spines are developed at the tip or on other portions of a leaf. The daggerlike leaf of the century plant is a striking example of a leaf whose tip is developed into a spine. Stipules are sometimes modified into stout spines (Fig. 107).

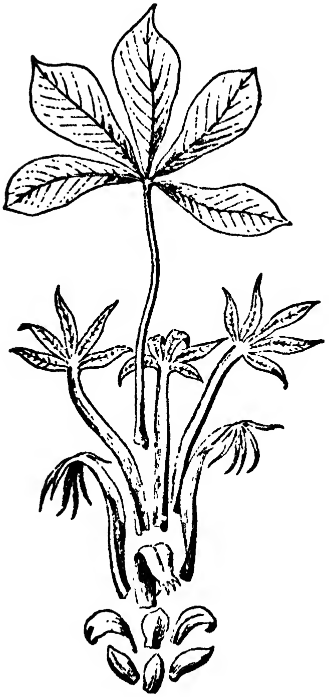

Fig. 110. Dissected bud of buckeye (*Æsculus macrostachya*), showing transitions from bud scales to leaves

Motile leaves. The leaf bases of many leaves and the bases of the leaflets of many compound leaves are modified into motile organs known as *pulvini*. These are most conspicuous in compound leaves, where the whole pinna hangs down and the leaflets fold together (Fig. 108) at night or when exposed to intense sunlight. Such movements are the result of the bending of the pulvini. The significance of the drooping and folding up at night (sleep movements) is not understood, but it has been suggested that these movements serve to reduce the radiation of heat from the leaves. When leaves droop and fold up while exposed to intense sunlight, such movements seem to be fitted to reduce the rate of transpiration. The leaves of the sensitive plant (*Mimosa pudica*) not only show sleep movements but also fold up and hang down as a result of contact or of shaking (Fig. 109). When the plant is shaken, the leaflets of all the leaves may fold together and the pulvini of the leaves bend so that the leaves hang down. These movements result in a very striking change in the aspect of the plant. Instead of having a luxuriant display of foliage, it becomes very inconspicuous. The significance of these movements is not clear, but they would seem to afford some protection from browsing animals.

Bud scales. We have seen that the tips of stems are protected by leaves. We also find that many deciduous plants have specially modified leaf structures which protect the buds during the season in which the tree is leafless (Fig. 114). These structures are known as bud scales, and may represent whole leaves, petioles with undeveloped blades, or stipules. In some cases there is in the same bud a series of transition forms from highly modified bud scales to leaves (Fig. 110). Bud scales are frequently covered with gummy or resinous substances and afford excellent protection to the bud.

The bracts which cover some types of unopened flowers are also modified leaves which have a protective function.

In this category we may also include the reduced leaves of parasitic and saprophytic plants. Such plants do not produce chlorophyll, and have only small reduced leaves whose only function would seem to be that of protecting the buds.

CHAPTER VIII

THE STEM

The chief function of the stem is to support the leaves and reproductive organs in such a manner that they can advantageously carry on their several functions. When we analyze this function of the stem, we find that several aspects must be considered. These can be grouped as attachment, position, and increase in number of leaves and reproductive organs.

Attachment. The stem furnishes any organ which it bears with a place of attachment, and thus enables that organ to maintain its position.

Position. In most cases, stems serve to distribute the leaves in such a manner that they do not shade each other to any great extent. Insect-pollinated flowers are usually in such a position that they are readily visible to the pollinating agents, while wind-pollinated flowers are so exposed that the pollen may be carried by wind from one flower to another. Stems support most fruits in such a way that they may be readily distributed by disseminating agents.

Increase in number. Many stems serve greatly to increase the number of leaves and reproductive organs that are produced by the plant. The stem, by increasing the number of leaves that the plant bears, enables the plant to produce more food and consequently a greater number of seeds.

Incidental functions. Besides the main function of support the stem has two important incidental functions: namely, to conduct water from the roots to the leaves and reproductive structures, and to carry food from the leaves to other parts of the plant. It is evident that if leaves and flowers were attached directly to the roots, there would be no need and no possibility for any other organ to conduct materials between roots and leaves.

The stem is frequently an important storage organ. During a large part of their lives many plants manufacture food faster than it is used; in most cases a large part of this surplus is stored in the stem. A stem is a better storage organ than an ordinary leaf, as it is usually a more permanent structure. Moreover, it is of advantage to the plant that the surplus food manufactured in the leaves is removed from them, so that food material does not accumulate and interfere with its continued production.

STRUCTURE OF STEMS

Nodes and internodes. The stem (Fig. 111) is composed of *nodes* (the places where leaves and branches originate) and *internodes* (the parts of the stem between the nodes). Branches usually originate at nodes, in the axils of the leaves that is, just above the point of attachment of the leaves).

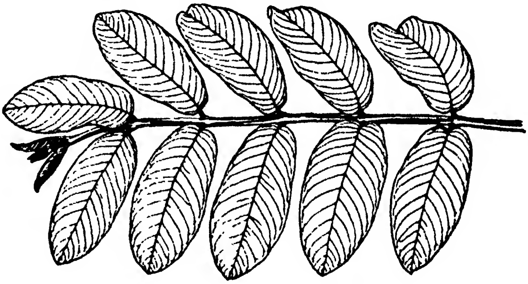

FIG. 111. Horizontal branch of guava (*Psidium guajava*). (× ⅓). See Fig. 116

Apical growth. The growth of a stem in length takes place largely, and in most cases only, at and near the tip. Very good evidence of this fact is afforded by an examination of an actively growing stem of a dicotyledonous plant (Fig. 111). It will be seen that all the leaves, except those near the tip, are of about the same size, and that the internodes are of approximately equal length. The similarity in size of the leaves shows that no new leaves are formed on the older parts of the stem, while the similarity in length of the internodes proves that when an internode has reached a certain length, elongation ceases. If all parts of the stem were to continue to grow in length throughout their existence, the internodes would be progressively longer toward the base of the stem. Near the tip of a growing stem (Figs. 15, 111) the leaves are very minute, while toward the lower part of the stem they are progressively larger until they reach mature size. The internodes near the tip are also very short, but away from the tip they become progressively longer until they also assume a definite length. The explanation of this is that new leaves and internodes are formed at the tip, and that they soon reach their mature length and then show no further growth in length. Growth at the tip of an organ is called *apical* growth.

The apical growth of a stem is due to the activity of a few actively dividing cells which are found at the very tip of the stem. This part of the stem is hidden by the young leaves produced near the tip, and cannot be seen until these leaves are removed (Fig. 112). A group of actively dividing cells is called *meristem.*

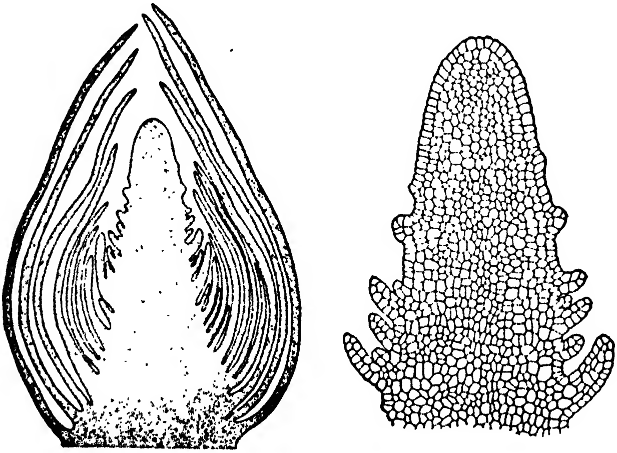

FIG. 112. Section through apex of the stem of a water plant

Left, through whole bud (× 60); right, through apex only (× 400)

Intercalary growth. In addition to apical growth some plants have another type of growth known as intercalary growth. This type of growth is very prominent in the stems of grasses. In grasses a group of cells just above each node remains meristematic for a considerable period of time and by division forms new cells, thus increasing the length of the internode. When the growing stem of a grass is pulled apart, it will usually break just above a node, where the soft meristematic tissue is located. This meristematic tissue in the grasses does not usually have enough strength to support the stem, but is reinforced by the sheathing leaf bases

(Fig. 93). This is evident when these leaf bases are removed, as the young stem will bend in the region of meristematic tissue. Even where intercalary growth is found it is not so important as apical growth, for apical growth produces new nodes and internodes, while intercalary growth only increases the length of the internodes to a limited extent.

Position of leaves. Leaves are formed only at the tip of a stem. They grow to mature size, perform their functions for a time, and finally fall from the stem. As no new leaves are formed on the older parts of a stem, the old portions of branches are always leafless, the leaves being confined to the smaller and younger portions. When leaves appear, on superficial observation, to arise directly from large trunks or branches, they really occur on short branches that are too small to be conspicuous.

Leaf scars. When leaves fall, they leave scars, known as leaf scars (Fig. 114), on the stem. These scars persist for a considerable length of time and mark the location of the nodes long after the leaves have fallen. In each scar are a number of more or less conspicuous dots, which in each species are arranged in a definite pattern. These dots mark the places where groups of xylem and phloem cells (called vascular bundles) passed from the stem to the leaf.

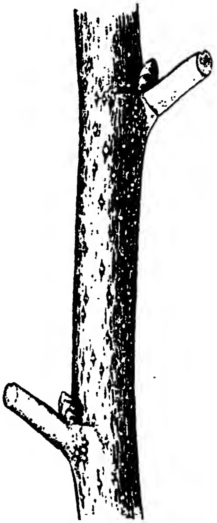

Fig. 113. Buds in the axils of leaves of mulberry (*Morus alba*)

The dots on the stem are lenticels. (× ⅘)

Buds. On stems that normally branch, buds are usually produced in the axils of all the leaves (Fig. 113). Buds are also found at the tips of stems, unless the bud has died or produced a terminal flower or flower cluster which has dropped off and ended the longitudinal growth of the stem. When the life of a terminal bud is ended by the production of a flower cluster, the continued growth of the shoot is due to one or more axillary buds. Buds are undeveloped shoots. After they are formed, they may either develop into shoots or remain dormant. A bud that has been dormant for a number of years may be forced to develop into a shoot by the removal of that part of the stem which is above the bud.

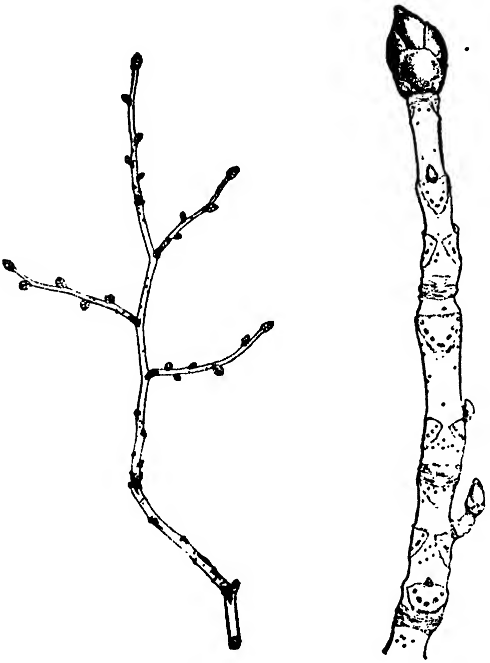

Fig. 114. Leafless branches of elm (left) and horse-chestnut (right), with winter buds protected by bud scales

The main branch of the elm has three rings of bud-scale scars, showing that the lower part of the branch is four years old; a ring of scars at the base of each side branch shows that these branches are the previous summer's growth (× ½). The branch of horse-chestnut also has three rings of scars, showing that the lower part of the branch is four years old (× ½)

Bud scales. Buds are protected by a covering of leaves. When deciduous trees are leafless for a considerable period, the dormant buds found on them during that time are usually covered by specially modified protecting leaves known as bud scales (Figs. 114, 110). These are described in the preceding chapter. When bud scales fall, they leave scars, just as do ordinary leaves. Usually, however, the scars of bud scales are considerably smaller and much more crowded together than are those of ordinary leaves. The result is that when the scales around a dormant bud fall, the crowded bud-scale scars frequently form a conspicuous ring around the stem and thus enable us to determine much of the history of that stem. A season's growth always begins just above a ring of bud-scale scars and ends with the formation of a new set of scales, so that by counting the rings of bud-scale scars we can tell the age of a branch. Also, by examination of the part of the stem between the rings we can tell how much growth was made during past seasons and the number of leaves borne by the branch during those seasons. The falling of leaves which results in leafless branches and also in the formation of rings of bud-scale scars may be connected with either a long cold season or a severe dry season (Fig. 115). Trees which do not shed their leaves may have their branches marked by rings of bud-scale scars if growth in length is seasonal and the buds are protected by scales.

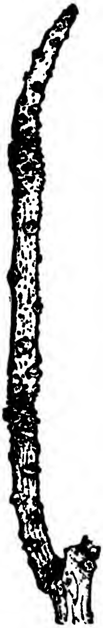

Fig. 115. A branch of the *Erythrina indica*, a tropical tree which is leafless during the dry season

This branch is marked by three rings of scars left by the falling of scales which protected the bud during successive dry seasons. The three rings show that the lower part of the branch is four years old. (× ¼)

When stems continue to grow and bear leaves throughout the year, there are of course no rings of bud-scale scars, and it is not possible to tell the age of a branch by inspection.

Lenticels. The epidermis of the very young parts of a stem contains stomata. As the stem grows older these are replaced by lenticels, which are groups of loosely arranged cells that allow an exchange of gases between the interior of the stem and the external atmosphere. On the younger internodes these can usually be seen as brownish spots with raised borders (Fig. 113).

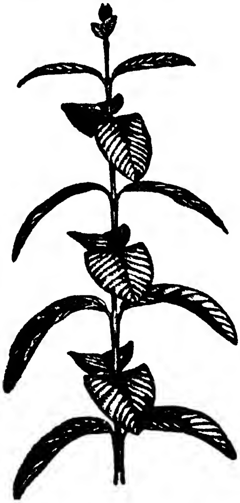

Fig. 116. Opposite leaves on an upright branch of guava (*Psidium guajava*)

Compare position of the leaves in Fig. 111. (× ⅓)

Arrangement of leaves. The leaves occur on the stem in a number of different arrangements. The system of leaf arrangement is known as *phyllotaxy*. When two leaves are attached opposite each other at the node, they are called *opposite* leaves (Fig. 116). On vertical stems each pair of opposite leaves is borne at right angles to the point of attachment of the pairs above and below it, so that the attachments of the leaves occur on the stem in four vertical rows, or ranks (Fig. 116). When three or more leaves are attached to the same node, they are designated as *whorled*. Whorled leaves are attached above and below points between the points of attachment of the leaves of neighboring whorls, except when there are irregularities in the whorls. If only one leaf occurs at a node, the leaves are said to be *alternate* (Fig. 194). Alternate leaves are arranged in a spiral around the stems, and the leaves have a definite location in the spiral. This location varies with different species.

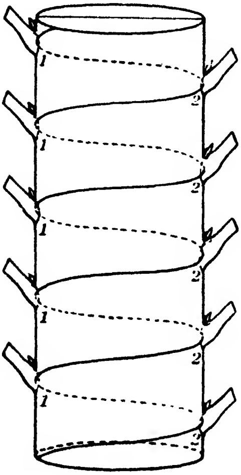

FIG. 117. Diagram showing the arrangement of two-ranked leaves

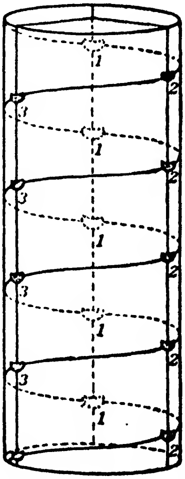

FIG. 118. Diagram showing the arrangement of three-ranked leaves

Phyllotaxy of alternate leaves. In some cases alternate leaves occur only on two sides of the stem, so that every leaf is above the second one below (Fig. 93). Such leaves are in two rows (two-ranked), and each leaf is halfway around the stem from the next in age (Fig. 117).

Another arrangement is in three ranks, in which the point of attachment of every leaf is directly above that of the third leaf below (Fig. 118) and there is a complete turn of the spiral for every three leaves. If we include the leaf which begins a turn of a spiral and also the one which ends it, there are, of course, four leaves; but when we take into consideration the whole length of the stem, there will be noted a turn for every three leaves.

The commonest arrangement is in five ranks, with the point of attachment of each leaf 2/5 of the way around the stem from that of the leaf next in age (Figs. 119, 194). In such arrangement the point of attachment of every leaf is directly above that of the fifth leaf below, and there are two turns in the spiral for every five leaves.

Still another method of arrangement is in eight ranks, with the point of attachment of every leaf 3/8 of the way around the stem from the next in age (Fig. 120). In this case the point of attachment of a leaf is directly above that of the eighth below, and there are three turns in the spiral for every eight leaves.

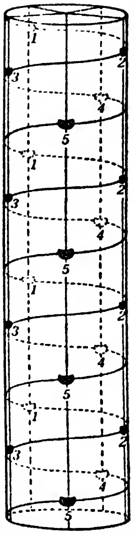

Fig. 119. Diagram showing the arrangement of five-ranked leaves

The top of the cylinder is marked off into five equal sectors. From the end of each line of division a line runs down the stem through a row of leaves, showing that the leaves are in five rows. The five vertical lines divide the stem into equal parts, so that the distance around the stem that one leaf is from the next in age (as from leaf 2 to leaf 3) can be determined. This distance is two fifths of the circumference, so that the divergence is 2/5. Between two consecutive leaves in the same vertical row there are two turns of the spiral

Divergence of alternate leaves. The proportion of the distance around the stem that a leaf is removed from the one next in age is called the *divergence*. When leaves are two-ranked (halfway around the stem from each other) the divergence is 1/2. We have just considered cases in which the divergence is 1/2, 1/3, 2/5, and 3/8. These figures, however, show other relations than the divergence. In the case of a divergence of 3/8 (Fig. 120) the denominator 8 shows the number of internodes between two successive leaves that are in the same vertical line on the stem, and also the number of vertical rows in which the leaves are arranged on the stem. The numerator 3 shows the number of turns of the spiral for every eight leaves. The same relation holds for all other divergences. In the case of 2/5 the denominator 5 shows the number of internodes between two successive leaves that are on the same vertical line and the number of rows in which the leaves are arranged. The numerator 2 shows that there are two turns in the spiral for every five leaves. When the divergence is 1/3, every leaf is above the third below, the leaves are arranged in three rows, and there is one turn of the spiral for every three leaves.

The greatest divergence that occurs with alternate leaves is 1/2, and the smallest is 1/3. All other divergences are intermediate between these two.

Series of divergences. The divergences for alternate leaves can be arranged in the following series: 1/2, 1/3, 2/5, 3/8, 5/13, 8/21, 13/34, 21/55, etc. Each fraction represents the part of the way around the stem that one leaf is from the next in age. In each fraction the denominator represents the number of internodes between successive leaves that are situated in the same vertical row, and also the number of vertical rows of leaves on the stem, while the numerator shows the number of turns of the spiral between two successive leaves in the same vertical row. It should be noted that the numerator and denominator for every divergence can be obtained by adding together those of the two preceding fractions in the series.

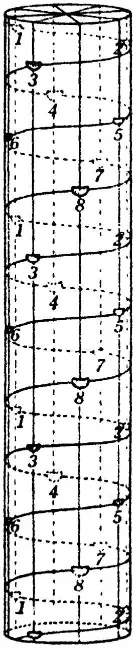

Fig. 120. Diagram showing arrangement of eight-ranked leaves

The first figure in the series, 1/2, is the greatest divergence that occurs with alternate leaves; the second figure, 1/3, is the smallest; the third figure, 2/5, is the second largest; the fourth figure, 3/8, is the second smallest; the fifth figure, 5/13, is the third largest; the sixth figure, 8/21, is the third smallest; the seventh figure, 13/34, is the fourth largest; and the eighth figure, 21/55, is the fourth smallest, etc. This can be expressed in a different way. If we take the first figure in the series and then every second figure, we obtain the following descending series of divergences: 1/2, 2/5, 5/13, 13/34. If we take the second figure in the series and then every other figure, we obtain the following ascending series of divergences: 1/3, 3/8, 8/21, 21/55. The divergences of these series expressed in degrees and minutes of circumference can be tabulated as follows:

1/2 = 180°	1/3 = 120°
2/5 = 144°	3/8 = 135°
5/13 = 138° 28	8/21 = 137° 8′
13/34 = 137° 39′	21/55 = 137° 27′

The largest figure in the ascending series is never as large as the smallest in the descending series, and both series approach the same limit, which is

a divergence of 137° 30′ 28″. The above figures for the ascending and descending series show that all members of the original series have values which lie within the limits 1/2 and 1/3. Likewise, the values for higher members than 3/8 lie between 2/5 and 3/8, and the values for higher members than 8/21 lie between 5/13 and 8/21. The difference between the divergences 13/34 and 21/55 is only 12′, or 1/5 of a degree, and the difference between any two higher members of the series must be less than this. There is, therefore, very little difference between the divergences of the higher members of the series. This relationship is shown in Fig. 121.

The phyllotaxy is frequently obscured by a twisting of the stem. A very striking case is that of the umbrella plant. Here the leaves are in three rows, but the stem is so twisted that the leaves radiate in all directions (Fig. 122).

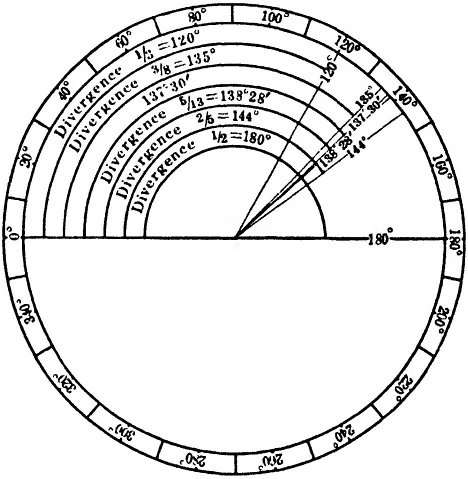

FIG. 121. Diagram showing the divergence of alternate leaves, expressed in degrees of circumference

All divergences lie between 1/3 = 120° and 1/2 = 180°, while all members of the series higher than 2/5 lie between 2/5 = 144° and 3/8 = 135°. The members higher than 5/13 lie so close to the theoretical limit of 137° 30′ that it is not practicable to show them on a diagram of this size

Branching. A great many stems branch and thereby increase the number of leaves and flowers which the stem can advantageously support. Since buds grow in the axils of the leaves, the arrangement of the branches would be the same as that of the leaves if all buds produced branches. Usually, however, many of the buds fail to grow. Some plants, as is the case with numerous palms (Fig. 123), do not branch at all. In many species the main stem continues to grow throughout the life of the plant and is very much more vigorous than any of the branches (Fig. 124). Plants that have this form of growth are said to be *excurrent*. In trees with excurrent growth the main trunk extends as a central shaft to the top of the tree, while the branches spread from it more or less horizontally. This results in a conical crown. The opposite form of growth is known as *deliquescent* (Fig. 125). In trees that have this form the main trunk is short, while the branches divide into smaller and smaller branches, producing a spreading crown.

Adventitious buds. Most branches originate from buds in the axils of the leaves and are called axillary branches. Buds may, however, arise from the internodes, the roots, or even the leaves (Figs. 101, 102), especially as the result of injury.

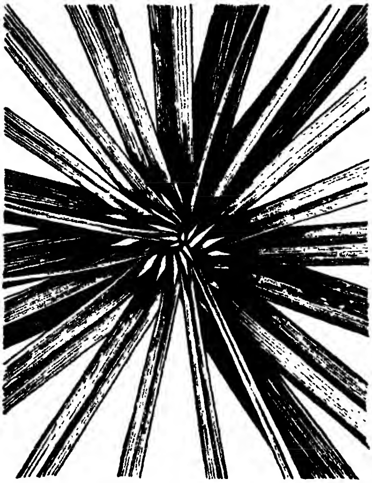

Fig. 122. Top view of a stem of the umbrella plant (*Cyperus flabelliformis*), showing three-ranked leaves on a twisted stem

The three rows of leaves can be traced by means of the axillary buds. (× ⅓)

Fig. 123. Coconut palms along a seacoast

Such buds are said to be adventitious buds, and the branches produced by them are adventitious branches. The growth of adventitious buds is made use of in the process of pollarding, that is, the cutting back of the tree to the trunk to promote a dense growth of branches which arise from the tissue produced around the wound. In the case of the willow, pollarding produces slender branches, which are used in making baskets. In propagation by root cuttings, which is practiced in some species, advantage is taken of the fact that some roots produce adventitious buds.

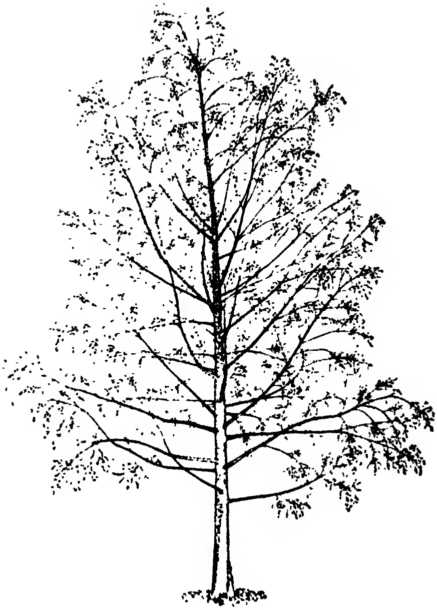

Fig. 124. Excurrent crown of *Casuarina*

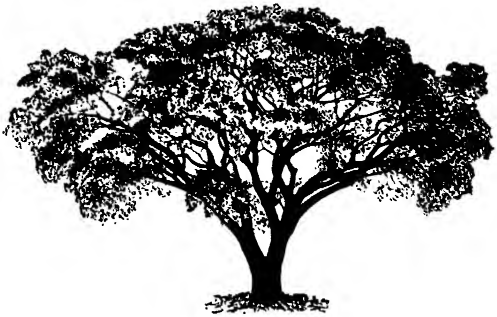

Fig. 125. Deliquescent crown of a rain tree (*Enterolobium saman*)

The rain tree is a native of tropical America and is one of the most widely used tropical trees. See Fig. 108

THE TWO TYPES OF STEMS

Flowering plants, as previously noted, are divided into two general classes, *monocotyledons* and *dicotyledons*. Monocotyledons are plants that have one cotyledon, or seed leaf, and dicotyledons those that have two cotyledons. The *cotyledons* are the first leaves produced by plants, and are usually found in the seed. When there are two they are opposite each other, but plants with two seed leaves frequently do not have their subsequent leaves opposite each other. The leaves of dicotyledons have netted veins (Fig. 16), while those of monocotyledons usually have parallel veins (Fig. 16). If a dicotyledon reaches any considerable size, it has a bark which can be readily stripped from the remainder of the stem, while monocotyledons do not have bark. Stems of monocotyledons reach a certain diameter and then do not usually become thicker, while stems of dicotyledons generally continue to grow in thickness as long as the plant lives. The floral parts of monocotyledonous plants are usually arranged in threes or in multiples of three, while in dicotyledonous plants the numbers vary, but they rarely occur in threes or multiples of three. The most important monocotyledons are grasses (including bamboos, sugar cane, and all cereals such as corn, rice, and wheat, but not buckwheat; sedges (plants which resemble the grasses in appearance); palms (Fig. 123); members of the lily family and related families; orchids; aroids; and members of the ginger (Fig. 206) and banana (Fig. 91) families. Dicotyledonous plants are much more numerous and include all ordinary trees, shrubs, and many small plants. The structure of the stem of a monocotyledonous plant is, as we shall see, very different from that of a dicotyledonous plant.

ANATOMY OF DICOTYLEDONOUS STEMS

General regions. In young dicotyledonous stems there are three distinct regions (Fig. 126). The outermost is the *epidermis.* Within the epidermis there is a zone that has the shape of a hollow cylinder and is known as the *cortex.* The center of the stem is occupied by a solid column, the *stele.*

Epidermis. The epidermis of the stem resembles that of the leaf very closely in both structure and function. It consists of a single layer of cells and is the outermost layer of the stem. It contains stomata and produces various types of trichomes. The outer cell walls are greatly thickened and heavily cutinized (Figs. 129, 130). The epidermis serves chiefly for restricting the rate of

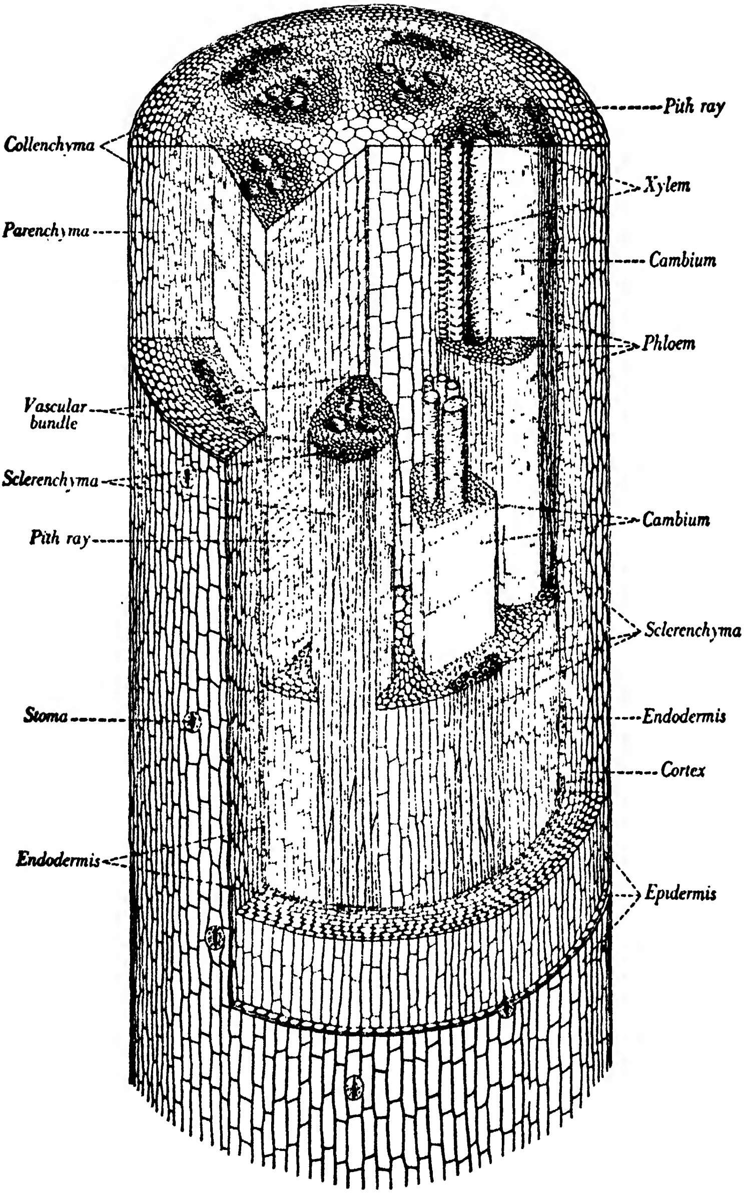

Fig. 127. Diagram of portion of an internode of a stem dissected in cross, radial, and tangential sections to show the various tissues of which it is composed

Parenchyma. The parenchyma cells of the cortex have the general structure and functions characteristic of parenchymatous cells (Figs. 126–130). Such cells are not highly specialized in structure for the performance of any particular function, but may be regarded as generalized cells which carry on to a limited extent all the usual functions of cells.

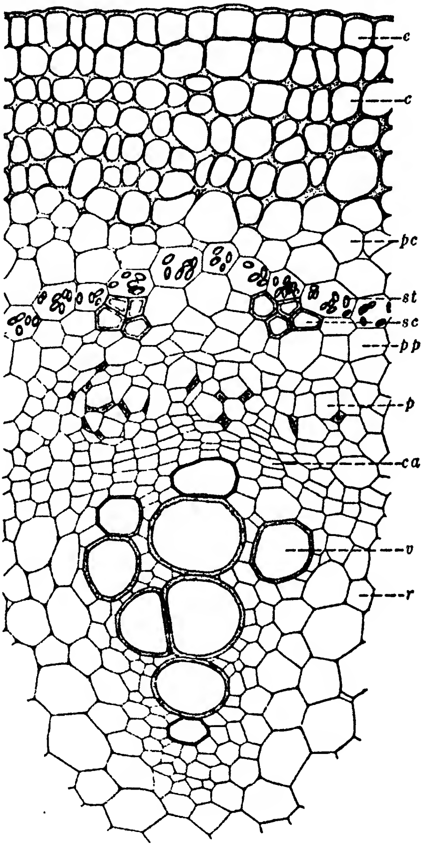

Fig. 128. Cross section of a portion of stem of castor-oil plant (*Ricinus communis*), showing a vascular bundle and the tissues around and external to it

e, epidermis; *c*, collenchyma; *pc*, parenchyma of cortex; *st*, starch sheath; *sc*, sclerenchyma of pericycle; *pp*, parenchyma of pericycle; *p*, phloem; *ca*, cambium; *v*, xylem vessel; *r*, pith ray. (× 180)

Parenchyma cells are ordinarily regular in shape, have comparatively thin walls, and are not greatly elongated in any direction. They are living cells and contain a moderate amount of protoplasm. When they are exposed to the light they develop chloroplasts and are known as chlorenchyma cells. Chlorenchyma cells are thus only a special kind of parenchyma cells. The parenchyma cells in the cortex of a stem are near enough to the light so that some or all of them develop chloroplasts and perform photosynthesis.

By being distended with water (turgid), parenchyma cells frequently help in giving rigidity to an organ. This function of parenchyma cells is important in succulent stems and in the young parts of the stems of woody plants before strong mechanical tissues have been developed. The rigidity produced by the turgor of the parenchyma cells is particularly useful in maintaining the form of the younger parts of herbaceous and climbing stems. It is of little or no help in dicotyledonous stems that have developed a massive column of wood.

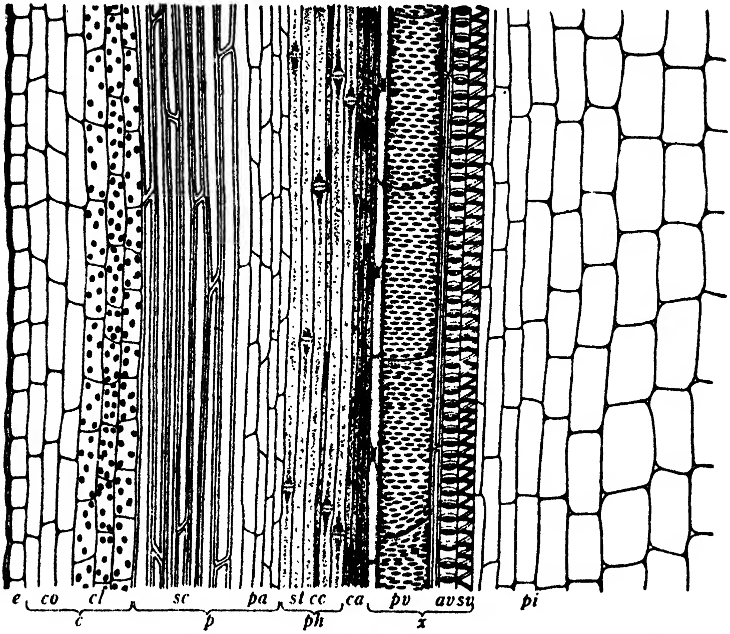

FIG. 129. Longitudinal section of a portion of a stem of *Aristolochia elegans*

e, epidermis; *c*, cortex; *co*, collenchyma; *cl*, chlorenchyma; *p*, pericycle; *sc*, sclerenchyma; *pa*, parenchyma; *ph*, phloem; *st*, sieve tube; *cc*, companion cell; *ca*, cambium; *x*, xylem; *pv*, pitted vessel; *av*, annular vessel; *sv*, spiral vessel; *pi*, pith. (× 190)

Parenchyma cells serve for the slow conduction of water and food. In the case of the cortex of the stem it is evident that the water which is received by the collenchyma and the epidermis must be conducted through the parenchyma.

The parenchyma is the special storage tissue of plants. In general the parenchyma of the cortex is less important than the parenchyma of the stele as a food-storage tissue, but food is frequently stored in it to some extent.

Collenchyma. On the inside of the epidermis there is usually a band of collenchyma (Figs. 126–130). The cells of the collenchyma are modified parenchyma cells with cellulose walls thickened at the angles where three or more cells are in contact (Fig. 27). The collenchyma resembles parenchyma in being alive and in having a moderate amount of protoplasm. The chief function of collenchyma cells is to serve as strengthening material in succulent organs which do not develop much woody tissue, or in the soft young parts of woody plants before stronger tissues have been developed. They are especially fitted for giving strength to young, growing organs, since the thickened parts of the walls have considerable rigidity, while the thinner parts allow for an exchange of materials between the cells and for the stretching and growth of the cells. The collenchyma cells of stems sometimes contain chloroplasts and carry on photosynthesis.

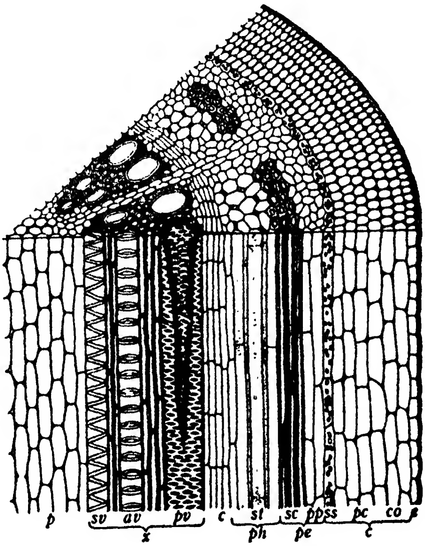

FIG. 130. Diagrammatic combined cross and longitudinal sections of stem

p, pith; *x*, xylem; *sv*, spiral vessel; *av*, annular vessel; *pv*, pitted vessel; *c*, cambium region; *ph*, phloem; *st*, sieve tube; *pe*, pericycle; *sc*, sclerenchyma; *pp*, parenchyma; *c*, cortex; *ss*, starch sheath; *pc*, parenchyma of cortex; *co*, collenchyma; *e*, epidermis

Sclerenchyma. Thick-walled dead cells known as sclerenchyma are found in the cortex of some stems. There are two varieties of these sclerenchyma cells: short or irregularly shaped cells, known as stone cells, and sclerenchyma fibers. Sclerenchyma fibers are long, thick-walled dead cells (Fig. 131) and serve as strengthening material. Stone cells give stiffness to the cortex and, when they form a more or less continuous layer, may take the place of the epidermis after the part of the cortex which is exterior to them has disappeared.

Stele of dicotyledonous plants. The part of the stem inside of the cortex is known as the stele (Figs. 126–130). This consists of three general regions. In the center is the *pith*, composed of thin-walled parenchyma cells. This central pith is surrounded by the *vascular-bundle region*, which is composed of *vascular bundles* separated by radial rows of parenchyma cells known as *pith rays*. Outside of this is the *pericycle*.

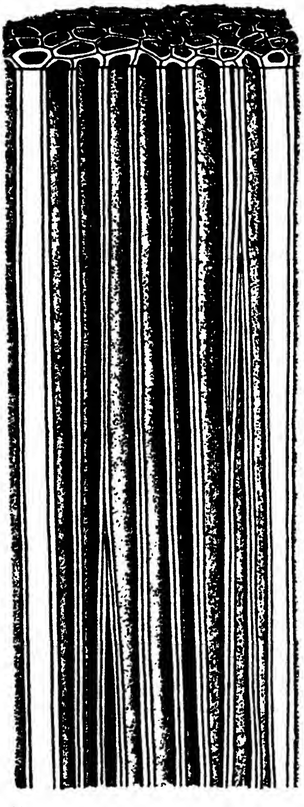

Fig. 131. Sclerenchyma fibers from a leaf of a century plant (*Agave cantula*). (× 300)

Pith. In a dicotyledonous plant the center of the stem is composed of thin-walled parenchyma cells and is known as the pith (Figs. 126, 129, 130). The cells of the pith are very similar to other parenchyma cells and have the same general functions. In perennial plants pith is frequently a transitory structure.

Vascular bundles. Around the pith are the vascular bundles, which, as seen in cross section, are arranged in the general form of a broken ring. Each consists of three parts (Figs. 126–130). That nearest the center of the stem contains thick-walled cells and is known as *xylem*. The peripheral portion of the bundle is composed of thin-walled cells called *phloem*. The xylem and phloem are separated by a *cambium layer*, which is composed of meristematic cells. By division the cambium layer increases the size of bundles by forming xylem cells on the inner side and phloem cells on the outer side. In some stems the bundles are separate and run the length of the internode. In others they are more or less united and form a hollow cylinder in which the pith rays occur as radiating plates with slight vertical extension (Fig. 165).

Xylem. The xylem which is formed before the activity of the cambium has begun to produce xylem and phloem cells is called primary xylem. This primary xylem is composed of two parts. The xylem formed first is nearest the interior of the stem and is called *protoxylem.* The more peripheral part of the primary xylem is known as *metaxylem.*

Xylem is composed of three different types of cells: namely, *tracheary cells,* which include tracheids and vessels; *wood fibers*; and *wood parenchyma.*

Tracheary elements. The *tracheids* are elongated dead cells, with walls that are thick in some places and thin in others. They serve to conduct water, or both as water-conducting and as strengthening cells. The thin places in the walls allow water to pass readily from cell to cell, while the thickened portions protect the cells from being crushed by the pressure of the surrounding tissues. As the tracheids are dead cells and without protoplasmic contents, they cannot develop turgidity, and so if the walls were uniformly thin the pressure of the neighboring cells would cause them to collapse. The walls of the tracheids are heavily impregnated with lignin. This material serves to strengthen them without greatly interfering with their permeability.

Vessels are composed of rows of tracheary cells the cavities of which are connected by the total or partial disappearance of the cross walls. The diameter of vessels is usually much greater than that of tracheids, and, as they form long tubes, they constitute the principal water-conducting elements of the dicotyledonous stem.

Tracheary cells may be divided into several types according to the method by which the walls are thickened (Figs. 129, 130). *Annular* tracheary cells have thickenings in the form of rings, while *spiral* tracheary cells have spiral thickenings. *Pitted* tracheary cells have walls which are uniformly thickened except for thin places in the form of pits. When the pits are long and narrow and lie horizontally one above the other, the tracheid or vessel is said to be scalariform, owing to the ladderlike appearance of the thickenings.

The protoxylem is composed largely of annular and spiral vessels and parenchyma, while the tracheary elements of the secondary xylem are pitted. Protoxylem is differentiated while the stem is elongating, and so the spiral and annular thickenings of the vessels are of special advantage, as they allow the vessels to be stretched. The metaxylem and secondary xylem are formed after increase in length has ceased, and therefore pitted tracheary cells are advantageous, as they have greater strength than spiral and annular ones.

Wood fibers. These are long, slender, pointed dead cells with greatly thickened walls and only comparatively few small pits (Fig. 132). They serve as strengthening cells. Tracheids that have a structure approaching that of wood fibers are called fiber tracheids. These two types of fibers usually make up a considerable proportion of the wood of dicotyledonous trees.

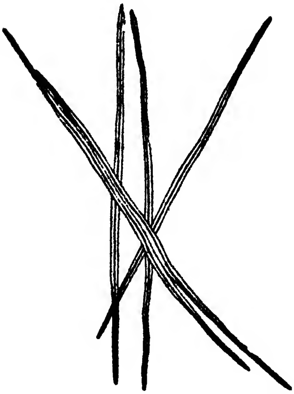

Fig. 132. Wood fibers from an oak (*Quercus bennettii*). (× 40)

Wood parenchyma. Parenchyma cells in the xylem are designated as wood parenchyma. They serve chiefly for the storage of food.

Phloem. The primary phloem of the dicotyledonous stems consists of three types of cells: sieve tubes, companion cells, and phloem parenchyma.

Sieve tubes. The sieve tubes consist of thin-walled, elongated cells arranged in vertical rows (Figs. 129, 130). The adjacent cells of a sieve tube are united by small holes in the cross walls (Fig. 133). Also, sieve tubes have rounded places on the side walls which are pierced by small holes and connect one sieve tube with another or with a companion cell. The areas on the walls of sieve tubes which contain such holes are called sieve plates. The sieve tubes get their name from the sievelike appearance of these plates. The walls of the sieve tubes are lined with a layer of protoplasm, but mature sieve tubes do not contain any nuclei.

The sieve tubes serve primarily for the conduction of food material. The holes which connect the cells of the sieve tubes make these tubes especially suited to the conduction of protein.

Companion cells. The companion cells are small cells which are attached to the sieve tubes. Each companion cell is the sister cell of a sieve-tube cell, the two being formed by the division of a mother cell. The exact function of the companion cells is more or less obscure; but since they are connected by sieve plates with the sieve tubes, which contain protoplasm but no nuclei, it would appear that the nuclei of the companion cells serve as nuclei for the sieve tubes. The small shaded cells in the phloem in Fig. 128 are companion cells.

Phloem parenchyma. The phloem contains parenchyma cells whose structure is very similar to that of other parenchyma cells. These are known as phloem parenchyma.

Cambium. While the other cells of the stem which are formed at the tip are being differentiated into permanent tissue, a single layer between the xylem and phloem remains undifferentiated (Figs. 126–130). This layer of meristematic cells is known as the cambium. The cambium consists of a single layer of cells which, by division, gives rise to xylem cells toward the center of the stem and phloem cells toward the periphery. The activity of the cambium cells thus enlarges the size of the bundles and, in consequence, that of the stem. This process is known as secondary thickening; it will be discussed in detail in a later section.

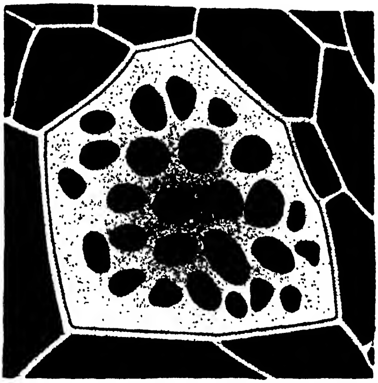

Fig. 133. A sieve plate of a squash stem (*Cucurbita maxima*) pierced by holes; walls of sieve tube; and surrounding cells. (× 110)

At first the cambium is confined to the bundles, but later the parenchyma cells of the pith rays which lie between the edges of the cambium in the bundles divide and form a layer of cambium which reaches across the pith rays and connects that in the bundles, so that the cambium becomes a continuous cylinder (Fig. 157). The beginning of this process is shown in Fig. 126.

Pith rays. The vascular bundles are separated from each other by radial rows of parenchyma cells (Figs. 126, 130) known as pith rays. The pith-ray cells are usually elongated in a radial direction.

They serve primarily for the conduction of food and water radially in the stem and for the storage of food. Food material which is stored in the wood parenchyma is conducted to these cells by the pith rays. The pith rays also serve for the conduction of water from the xylem toward the other parts of the stem. If a pith ray from an old stem is stained with iodine, it will usually be found to contain numerous starch grains.[1]

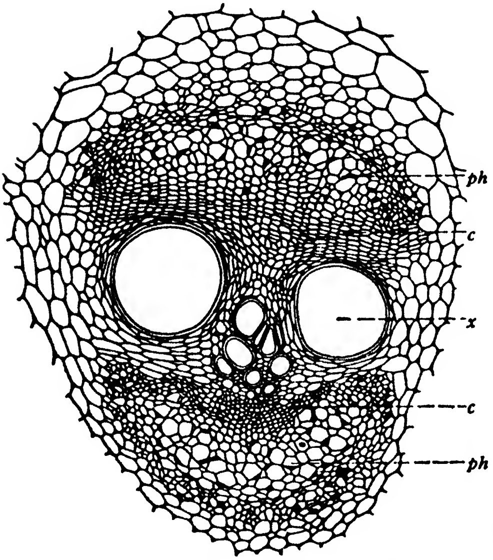

FIG. 134. Cross section of a bicollateral bundle of a squash stem, showing phloem on both sides of the xylem. (× 95)

ph, phloem: *c*, cambium region; *x*, xylem vessel

Pericycle. The region between the vascular bundles and the cortex is known as the pericycle. It is ordinarily composed of parenchyma and sclerenchyma cells, but the sclerenchyma cells may be absent. The sclerenchyma may occur as separate patches (Figs. 128, 130) or as a continuous ring in the outer part of the pericycle (Fig. 126), forming a sharp line of demarcation between the stele and the cortex. The sclerenchyma cells in the pericycle are like other sclerenchyma cells (Fig. 131) in being long, thick-walled dead cells which serve as strengthening material.

Variations in stem structure. The above description of the structure of stems applies to the great majority of dicotyledonous

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[1] The term *wood ray* is proposed in place of *pith ray* by some modern anatomists, on the ground that these rays do not belong to the pith, but that the parts of the rays between the primary xylem represent tracheids which have been transformed into parenchyma cells. Owing to the widespread use of the term *pith ray* in literature it seems convenient to retain it, even though from the standpoint of origin it may be inappropriate.

plants, but there are a few which show minor variations. If these few exceptional cases are left out of consideration, the general structure of dicotyledonous stems is remarkably uniform. The relative development of the various parts, however, varies greatly in different species. In some cases the pith is wide, while in others it is narrow. It may be wide and transitory and its early disappearance result in a hollow stem. The vascular bundles vary considerably in number and size, while the pith rays and cortex vary in width. Thus, while there is a remarkable uniformity in the general plan of the dicotyledonous stem, there are at the same time considerable differences in detail.

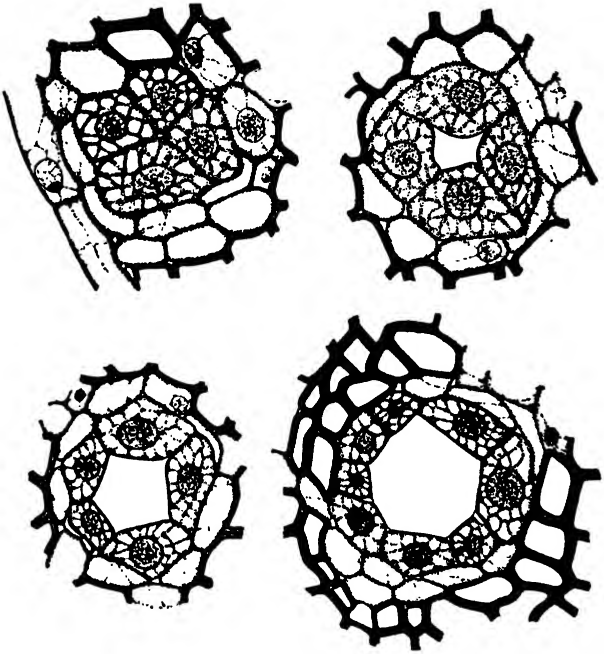


FIG. 135. Successive stages in the formation of a resin duct in pine. (× 250)

Bundles which have the phloem only on the outside of the xylem are called *collateral* bundles. The bundles of some plants have phloem on both the outside and the inside of the xylem (Fig. 134) and are known as *bicollateral* bundles.

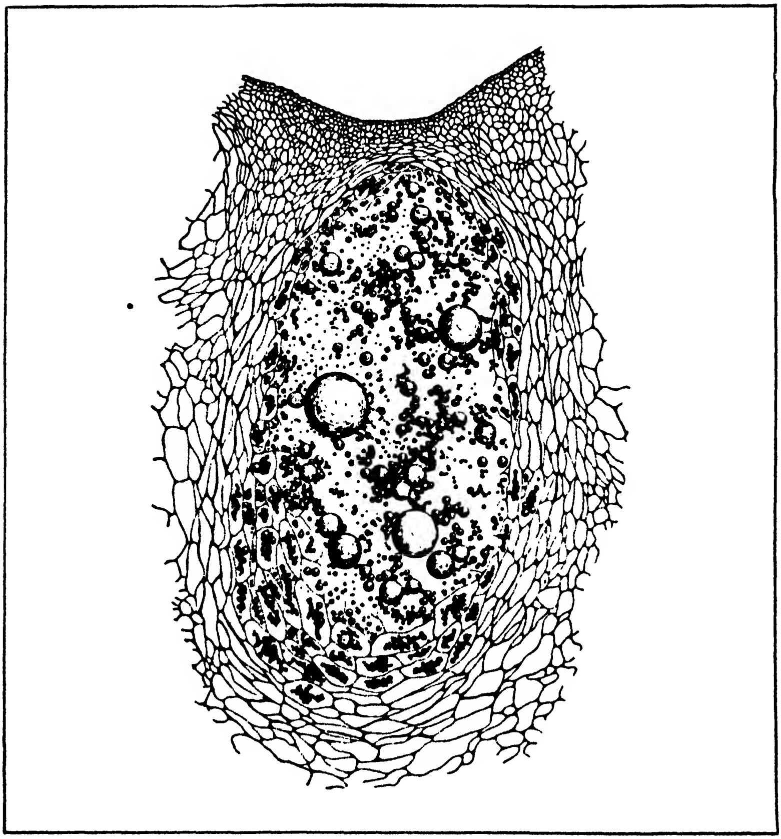


Fig. 136. Longitudinal section of oil gland in orange peel. (× 450)

Resin ducts. Many plants contain intercellular passages filled with resinous substances and known as resin ducts. They are formed either by the separation of neighboring cells (Fig. 135) or by the disintegration of cells. Turpentine is obtained by cutting through the resin ducts of pine trees, after which the turpentine exudes and is collected. Various kinds of varnish and other resins are obtained by the same method from other trees.

Resin ducts are, essentially, long passages surrounded by glandular cells. They occur not only in stems but also in other parts of plants.

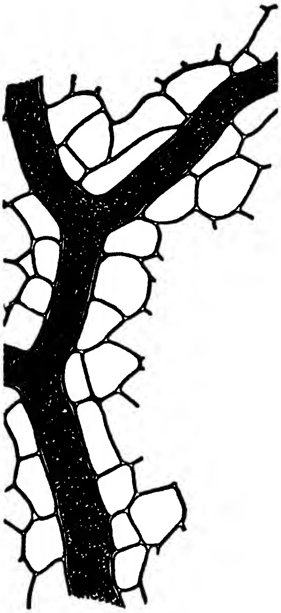


FIG. 137. Latex tube of poinsettia (*Euphorbia pulcherrima*). (× 125)

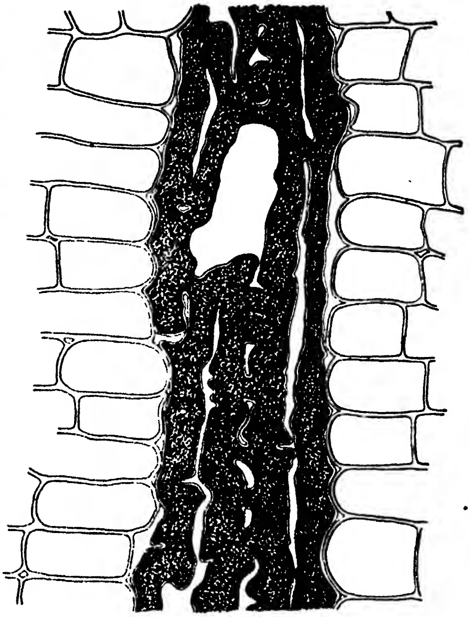


FIG. 138. Network of latex tubes of a rubber tree (*Manihot glaziovii*)

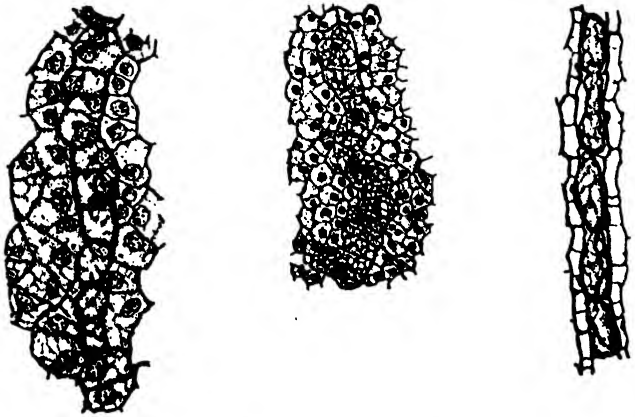


FIG. 139. Stages in formation of latex tube in *Achras sapota*, the tree that yields the gum which is the basis of chewing gum (see Fig. 357). (After Karling)

Internal glands. Resin canals are one type of internal gland, of which a number of other forms occur in various plant organs. Internal glands frequently contain essential oils. These oils are volatile and are usually very odoriferous. Well-known examples are eucalyptus oil and the oil from orange peel. The latter occurs in large oval glands. These glands originate in the splitting apart of certain cells, but are formed largely by the breaking down of cells containing the oil. The disintegration of the cells brings the oil into the large cavity of the gland (Fig. 136).

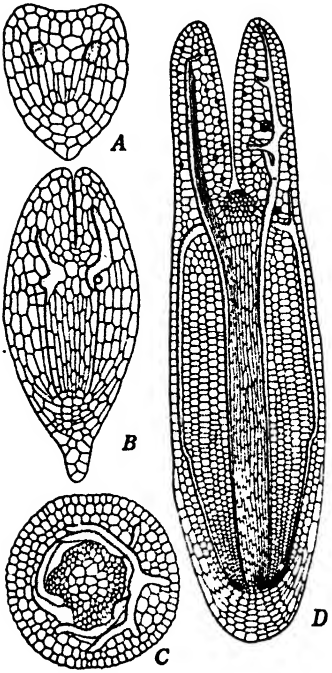


Fig. 140. Growth of latex tubes in developing embryo of *Euphorbia exigua.* All sections are longitudinal except the lower left, which is a cross section. (After Chauveaud)

Latex tubes. Milky juice (latex) is found in long branching tubes known as latex tubes (Fig. 137). In many cases neighboring tubes become connected, thus forming a network (Fig. 138). When these tubes are cut, the latex exudes as a milky-looking watery juice, generally white. Rubber, gutta-percha, opium, gum chicle (the chief base of chewing gum), and other valuable substances are derived from coagulated latex. The tapping of rubber trees consists in cutting the tubes and allowing the latex to exude.

Latex tubes are formed in two very different ways. In some cases rows of cells lose their cross walls and become transformed into latex tubes (Fig. 139); as in Pará rubber (*Hevea brasiliensis*). In other cases the tubes are not part of the tissues produced from either the apex of the stem or the cambium, but result from the growth of tubes found in the seedling (Fig. 140). As the stem grows in length, or as other organs are formed, these latex tubes also grow and push their way between the cells of the newly formed tissues.

Summary of Principal Tissues in a Dicotyledonous Stem

- Epidermis
  - Epidermal cells
  - Guard cells
  - Trichomes
- Cortex
  - Collenchyma
  - Parenchyma
  - Starch sheath
- Stele
  - Pericycle
    - Parenchyma
    - Sclerenchyma
  - Pith rays
    - Parenchyma
  - Pith
    - Parenchyma
  - Vascular bundles
    - Phloem
      - Sieve tubes
      - Companion cells
      - Phloem parenchyma
    - Cambium
      - Meristematic cells
    - Xylem
      - Tracheary cells
        - Vessels and Tracheids
          - Spiral
          - Annular
          - Pitted
      - Wood fibers
      - Wood parenchyma

ANATOMY OF MONOCOTYLEDONOUS STEMS

Monocotyledonous stems are similar to dicotyledonous stems in having an epidermis, a cortex, and a stele. The cortex may be well developed and sharply marked off from the stele, or it may be very narrow and inconspicuous (Fig. 141). It is in the structure and arrangement of the bundles that monocotyledonous stems differ markedly from dicotyledonous stems.

Stele. The vascular bundles of monocotyledonous stems, instead of being arranged in a cylinder as in dicotyledonous stems, are usually scattered throughout the stele, including the pith, so that there is no distinction between pith and pith rays (Figs. 141, 142). Sometimes the center of the stele is free from vascular bundles and is occupied by parenchyma cells, which dry up and disappear at an early stage, resulting in a hollow stem, as in most grasses, including most bamboos.

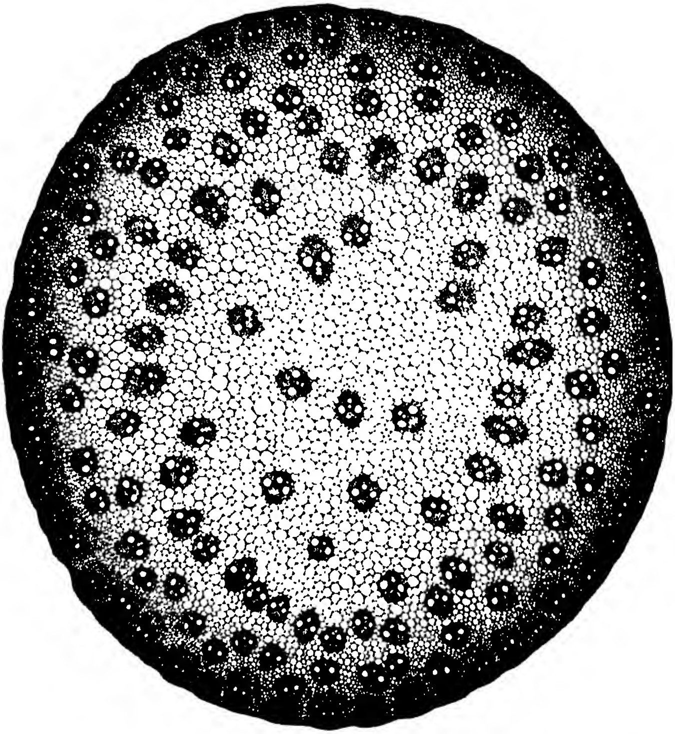


Fig. 141. Cross section of a monocotyledonous stem, *Zea mays*. The dark oval areas are cross sections of vascular bundles. The cortex is a thin layer composed of one or two layers of cells between the epidermis and the outermost series of vascular bundles

Vascular bundles. The vascular bundles of monocotyledonous stems are like those of dicotyledonous stems in consisting of xylem toward the center of the stele and phloem toward the periphery. They differ, however, in not having a cambium layer, such as is found in dicotyledons (Fig. 143). This is connected with the fact that monocotyledons usually do not have secondary thickening. Each bundle is generally more or less completely surrounded by a sheath of sclerenchyma cells, the *bundle sheath* (Figs. 143, 144), which is particularly well developed on the sides toward the center and toward the periphery of the stem. The phloem is made up mostly of sieve tubes and companion cells, and the xylem of vessels and wood parenchyma.

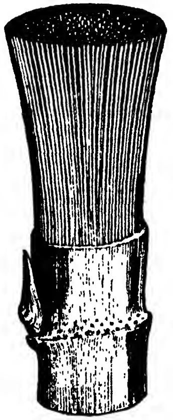


Fig. 142. Vascular bundles dissected out of an internode of sugar cane. (× ½)

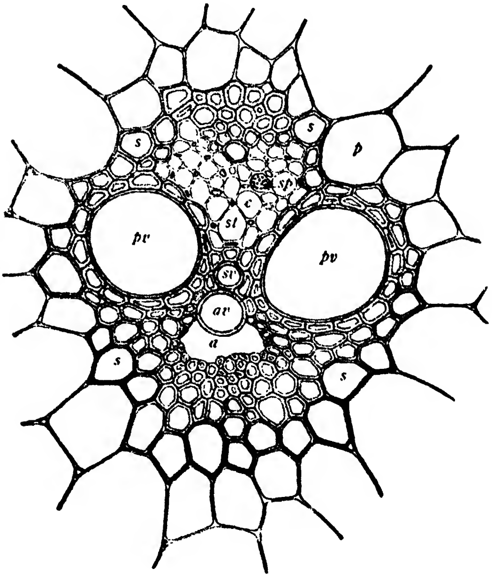


Fig. 143. Cross section of a vascular bundle of sugar cane (*Saccharum officinarum*)

p, parenchyma; *s*, sclerenchyma of bundle sheath; *a*, air space; *ar*, annular vessel; *sv*, spiral vessel; *pv*, pitted vessel; *st*, sieve tube; *sp*, sieve plate; *c*, companion cell. (× 185)

The strands of sclerenchyma around the bundles of some plants are extracted and used in various ways as fibers. Maguey and sisal fibers are the strands of sclerenchyma around the bundles of the leaves of species of *Agave* (Fig. 131), while abacá (Manila hemp) is composed of similar strands from the leaf bases of *Musa textilis*, a plant which is almost identical with the banana in appearance.

The arrangement of the different elements in the bundles of corn and sugar cane is characteristic of many monocotyledonous bundles (Figs. 143, 144). In these cases the bundles are surrounded by a sclerenchyma sheath which is widest on the sides toward the center and toward the periphery of the stem. On the side near the interior of the stem, just within the bundle sheath, there is usually a conspicuous air space. Next to this there are frequently two elements of the protoxylem; the first is an annular vessel and the second is a spiral vessel. On both the right and the left side of the bundle is found a large vessel which is pitted or narrowly reticulate. Between the larger vessels are smaller, tracheary elements. The phloem is next to the peripheral part of the bundle sheath and contains conspicuous sieve tubes and companion cells.

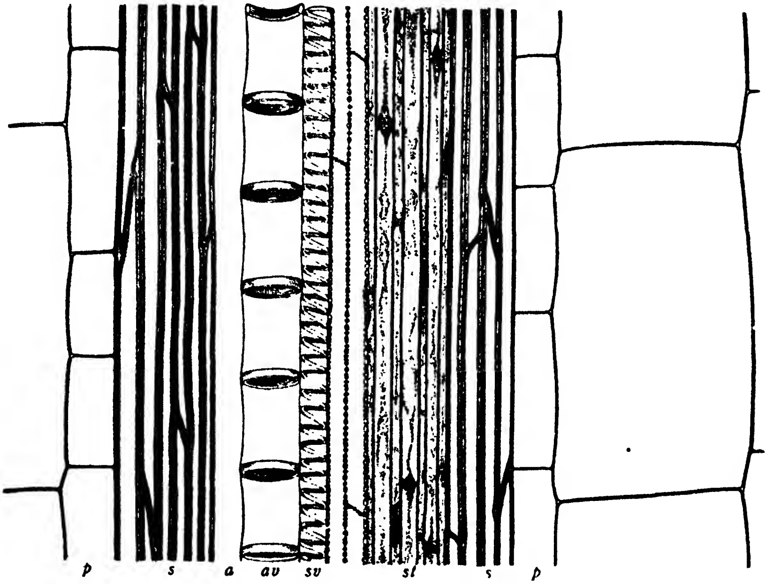


Fig. 144. Longitudinal section through a vascular bundle of sugar cane (*Saccharum officinarum*)

p, parenchyma; *s*, sclerenchyma of bundle sheath; *a*, air space; *av*, annular vessel; *sv*, spiral vessel; *st*, sieve tube. (× 150)

The number of vessels varies in monocotyledonous bundles. In many cases there is only one large vessel, instead of two as in corn and sugar cane.

COURSE OF BUNDLES IN STEMS

A bundle extends up the stem and then passes out into a leaf. The bundles from leaves in the upper part of the stem enter the stem, pass down, and at a lower node join with other bundles. In this way the vascular elements in the stem become connected with new leaves. At the nodes bundles branch and branches of different bundles coalesce (Fig. 145).

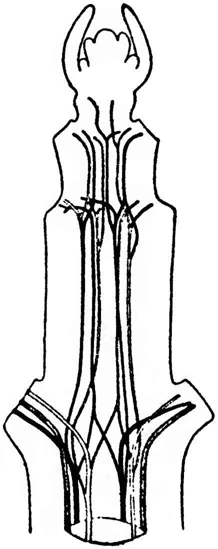


Fig. 145. Course of bundles in stem of *Clematis verticellaris*

Modified after Nagali

ANATOMY OF CONIFEROUS STEMS

In coniferous stems the general arrangement of the various tissues is very similar to that in dicotyledonous stems. The same type of secondary thickening occurs in both kinds of stems. The most conspicuous differences are that the xylem of conifers contains only tracheids and wood parenchyma, and that companion cells are not found in the phloem.

Since the xylem of conifers does not contain fibers or vessels (Fig. 146), the tracheids serve both as water-conducting and as strengthening elements. Tracheids are not so well fitted for conducting water as are vessels. The small size and xerophytic structure of coniferous leaves (Fig. 991) probably have some connection with the absence of vessels in coniferous stems. Most coniferous trees (Figs. 990, 995, 260) retain their leaves for several years — in temperate countries throughout the long, cold winter, when the dicotyledonous trees lose their leaves. In the discussion of leaves it was pointed out that the loss of leaves by deciduous trees is a method of restricting the rate of transpiration at times when the roots are not able to absorb enough water to replace that which would be lost by the foliage. The deciduous tree without its leaves is one of the most perfectly protected of plant structures, since all the exposed portions are effectively covered by the impervious bud scales and bark. The low rate of transpiration from coniferous leaves is probably connected with the ability of these trees to retain their foliage throughout the cold winter. At such times coniferous trees have some advantage over dicotyledonous ones in that they can carry on photosynthesis. In the tropics conifers very rarely occur at low elevations, while they flourish in high mountainous regions where the rate of evaporation is always low.

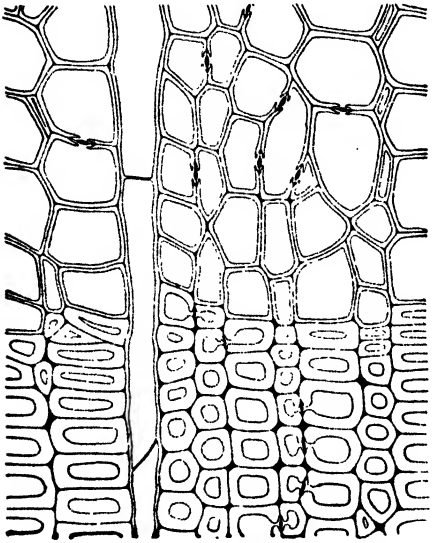


Fig. 146. Cross section of a small portion of the wood of a redwood tree, showing xylem on both sides of a pith ray

The small cells in the lower part of the drawing are the last of the wood cells formed during a summer, while the large cells above them are the first xylem cells formed during the next spring. The fact that much larger cells are formed in the spring than later in the summer results in the marking of the wood by annual rings of growth. (× 275)

ARRANGEMENT OF MECHANICAL TISSUES

Mechanical tissues. The plant body obtains strength from three general types of cells:

1. *Parenchyma cells*, whose rigidity is due almost entirely to osmotic pressure. Parenchyma tissue is weak and so must be present in considerable bulk in order to give any great amount of strength.

2. *Collenchyma cells*, which are living cells and have their walls thickened at the angles where three or four cells meet (Fig. 27). These cells get their rigidity from the thickened walls as well as from turgor, and are therefore much better strengthening material than are parenchyma cells. As they are living cells whose walls can be stretched, they are especially fitted for strengthening the growing portions of a plant.

3. *Thick-walled dead cells* (Figs. 131, 132), including the sclerenchyma of the cortex and pericycle and the wood fibers. The wood fibers are elongated dead cells with very thick walls. Sclerenchyma cells are stronger than parenchyma or collenchyma cells, and are the principal strengthening material of old stems. As they are dead cells with very thick walls, they are not suited to give strength to growing parts. Thick-walled tracheids may be very similar to sclerenchyma in their mechanical property.

Girders. The arrangement of the strengthening material is different in leaves, in stems, and in roots, and is suited to the special stresses which these various organs have to withstand. In order to understand this arrangement it will be convenient to consider the stresses occurring in a girder, or beam. If a beam of wood or other material is supported at both ends and is weighted in the middle, the upper surface will be subjected to compression and the lower surface to tension, or stretching. Going from the upper surface to the lower, we find that the compression decreases as the center is approached and at the center it becomes zero. The stress is then changed to tension, which gradually increases toward the lower surface. It will thus be seen that the greatest stresses in a beam are at the upper and lower surfaces and the least stress is in the center. For this reason it is usual to construct a beam in such a manner that it is more massive or composed of stronger material at the upper and lower surfaces than in the center. A usual form is the I-beam (Fig. 147). In this case the material is expanded at the upper and lower surfaces and connected by a much narrower portion. The extensions at the surfaces are called *flanges*. In bridge construction the connecting portion, known as the *web*, is frequently made of latticework.

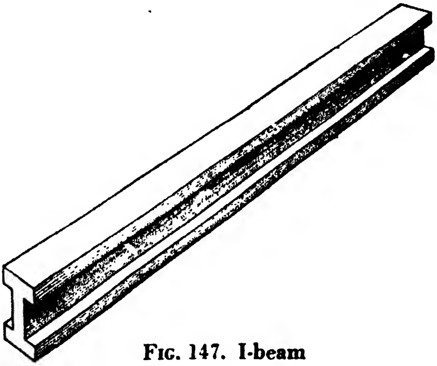


FIG. 147. **I-beam**

The wide portions at the top and bottom are the flanges; the narrow connection is the web

Mechanical tissues in leaves. In a leaf we have different conditions from those just discussed, in that the leaf is supported at only one end. The weight of the leaf gives it a tendency to bend downward so that its upper surface is stretched, or under tension, while its lower surface is under compression. As in the other case, the greatest stresses are at the upper and lower surfaces and the least stress is in the center. This arrangement, therefore, calls for longitudinal girders in which the strongest material is near the outer surfaces. The midrib and larger veins of the leaf represent the girders. The principal strengthening material in these is usually collenchyma, and this is generally found as a broad band near the upper and lower surfaces just within the epidermis (Fig. 26). The collenchyma, therefore, represents the flanges of an I-beam, while the tissues between the two bands of collenchyma represent the web. The larger veins of grasses usually have sclerenchyma near the upper and lower surfaces, and so act as girders (Fig. 33).

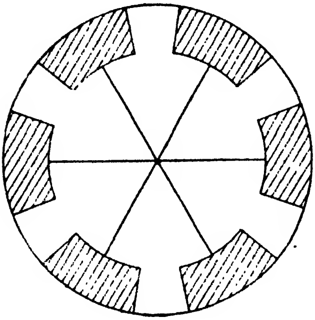


FIG. 148. Diagram of cross section of a compound girder composed of I-beams, the webs of which have a common center

Mechanical tissues in stems. If a column, such as a tree trunk, were supporting an evenly distributed weight, the manner in which the strengthening material was arranged would, theoretically, make comparatively little difference. The only stress would be a downward pressure, or compression, the resistance to which would depend more on the cross-sectional area than on the arrangement of the strengthening material. Actually, however, such a condition is seldom attained. When in addition to the vertical pressure of gravity there is a sidewise pressure, as that of wind or of an animal,

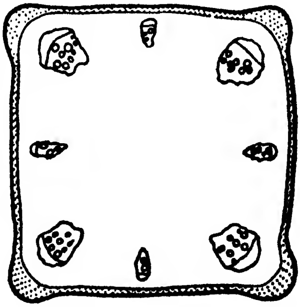


FIG. 149. Diagram showing arrangement of vascular bundles and collenchyma (dotted area) in a four-cornered stem

the side toward the pressure tends to become stretched, or develops tension, and the opposite side is subjected to compression. So too when the stem of a plant becomes inclined, as by the action of the wind or by the weight of the branches, the side that is uppermost is under tension and the lower side under compression. It therefore becomes important to have the strengthening material distributed near the upper and lower surfaces, or, in other words, in the form of an I-beam. As the plant is likely to bend in any direction, however, and thus may develop stress on any side, it is advantageous to have a number of these girders, with the webs crossing each other and the center of each at the center of the stem (Fig. 148).

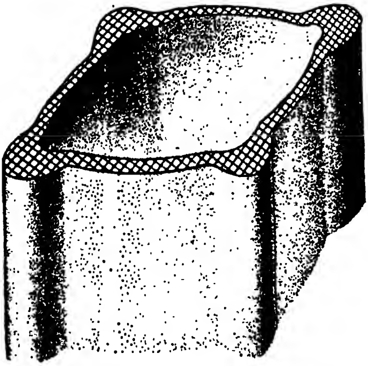


Fig. 150. Diagram showing shape of collenchyma in a four-cornered stem

In the four-cornered stems of such plants as the mints or coleus the corners are occupied by a conspicuous development of collenchyma (Figs. 149, 150), which thus forms the flanges of two I-beams, the webs of which are crossed. The large vascular bundles are near the corners, so that the phloem is protected by being between the xylem and the collenchyma. In many plants there are strands of sclerenchyma outside of each vascular bundle (Fig. 151), and in such cases two strands on opposite sides of the stem represent the flanges of an I-beam. This sclerenchyma which is near a bundle not only serves as one of the flanges of an I-beam but also is in a position to protect the delicate elements of the phloem. When

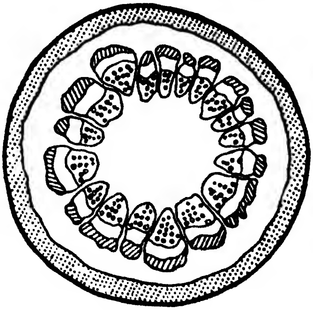


Fig. 151. Diagram of a dicotyledonous stem, showing sclerenchyma (hatched areas) just outside of each bundle, and collenchyma (dotted area) forming a hollow cylinder within the epidermis

the edges of the flanges of such a compound girder as that shown in Fig. 148 are connected, there is no necessity for the webs; and if they are absent, a hollow cylinder results. This type of construction is very frequently found in plants and is particularly evident in hollow stems, such as those of most grasses. In many plants the sclerenchyma is arranged in the form of a hollow cylinder (Figs. 126, 153). Such hollow cylinders are, as a rule, near the outer surface of the stem. The strengthening material of the growing part of a stem is usually collenchyma, and this is generally arranged in the form of a hollow cylinder just within the epidermis (Figs. 151, 152, 153).

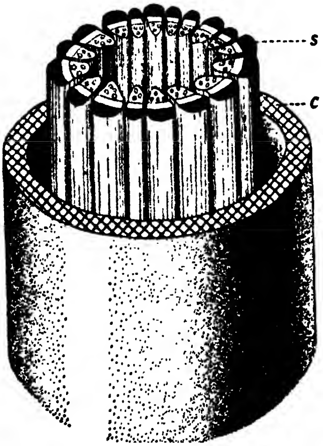


Fig. 152. Diagram showing arrangement of collenchyma (c), forming a hollow cylinder at the periphery of the stem, and of sclerenchyma (s), exterior to each vascular bundle and forming an interrupted cylinder. (Compare with Fig. 149)

The foregoing discussion of the arrangement of the strengthening material in the stem applies particularly to herbaceous and young stems. In the case of trees the development of a massive column of wood takes the place of the strengthening material that was used in the young stem.

Tissue tensions. The location of thick-walled mechanical cells near the periphery of an organ with thin-walled parenchyma cells in the center gives rigidity in another manner besides that just considered. Thick-walled cells, particularly dead sclerenchyma cells, offer considerable resistance to any tendency to stretch them. On the other hand, thin-walled parenchyma cells tend to stretch, owing to their turgidity. The stretching of the parenchyma is, however, checked by the strong, thick-walled cells, which are themselves under tension owing to the tendency of the parenchyma to stretch them. These two strains, working against each other, produce rigidity in somewhat the same way as in a turgid cell, in which the contents, which have a tendency to swell, are compressed by the stretched cell wall, or as in a rubber tube when air or water is compressed within the tube. The compression of inner by outer tissues can very easily be demonstrated with stems or petioles of many herbaceous plants. Fig. 154 shows a piece of a large petiole which was cut off evenly at both ends, after which the outer and inner parts were separated at the upper end by a cylindrical cut. The central portion, which was under compression, being freed from the outer part, elongated and so projected beyond the latter, which contracted slightly.

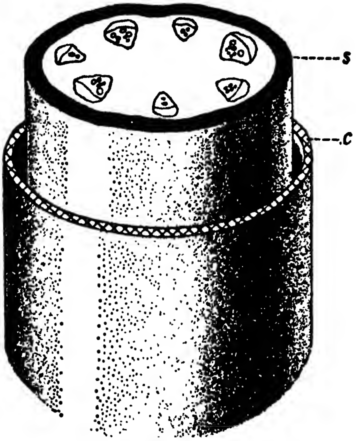


FIG. 153. Diagram showing arrangement of collenchyma (*c*), forming a hollow cylinder at the periphery of the stem, and sclerenchyma (*s*), forming one exterior to the bundles. (Compare with Fig. 151)

Mechanical tissues in monocotyledonous stems. In many monocotyledonous plants the arrangement of the strengthening material is very similar in principle to the reinforcing of concrete in a concrete structure. The concrete withstands compression, while the iron rods withstand the tension due to movement etc. In monocotyledonous plants the parenchyma withstands the compression, while the sclerenchyma strands, which are connected with the vascular bundles, withstand the tension (Fig. 141). A very excellent example of this is abacá, or Manila hemp. This plant, whose appearance and structure are almost identical with those of the banana (Figs. 91, 92), has a massive trunklike portion composed largely of the soft tissues of the leaf bases, through which run the long sclerenchyma strands that are the abacá of commerce. The sclerenchyma can withstand considerable tension, while the massive development of parenchyma withstands the compression.

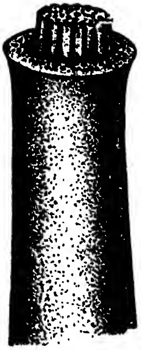


FIG. 154. Demonstration of tissue tension in a petiole of elephant's-ear (*Alocasia indica*). (× ⅔)

Mechanical tissues in roots. The roots of a plant serve to anchor it in the ground. They act like cables, and the principal stress to which they are subjected is longitudinal tension, or pull. It is evident that when a plant is blown by the wind the roots on the side from which the wind is coming are subjected to longitudinal tension, and if they are not strong enough to withstand this they break and the plant is blown over. The best arrangement of material to withstand this type of stress is in the form of a cord. In roots the vascular bundles and strengthening materials are usually much more centrally located than they are in the stem, the center being frequently occupied by thick-walled elements. Compare Figs. 126 and 225.

MOVEMENT OF MATERIALS IN STEMS

Food materials. Proteins dissolved in water travel in the sieve tubes. The direction of the movement may be either up or down, according to where the protein is to be used or stored.

The carbohydrates travel in the phloem. What has been said of the direction of movement of proteins applies also to the carbohydrates. The carbohydrates move from cell to cell only when they are in solution in water.

Carbohydrates in vessels. While carbohydrates usually move in the phloem, they are frequently found in considerable quantities in the vessels when food material is being transported on a large scale from storage regions to rapidly growing organs, as in deciduous trees at the beginning of the period of growth, when the leaves are expanding. In such cases the carbohydrates diffuse from the parenchyma into the vessels and are carried upward to the expanding foliage or inflorescences. This is conspicuously true of the sugar maple, and explains why a solution of sugar is obtained from this tree by boring into the wood in the spring. A similar phenomenon is observed in the exudation of sweet sap from tapped inflorescence stalks of palms, such as the coconut (Figs. 155, 156). Such sap is frequently used for manufacturing alcohol or sugar.

Water. The movement of water upward in the stem takes place in the vessels. This can be very clearly shown by cutting off a stem and placing the lower end in a colored solution. If the stem

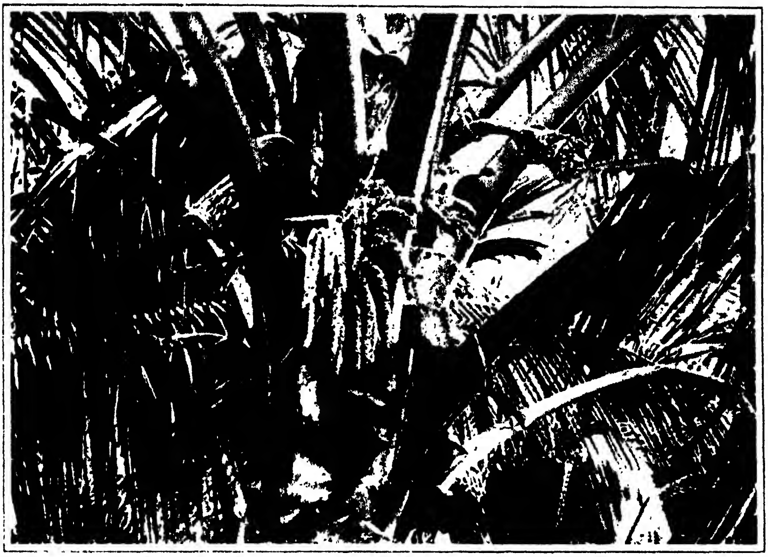


FIG. 155. Coconut palm with inflorescences cut and bound to be inserted in bamboo joint for collecting sweet sap

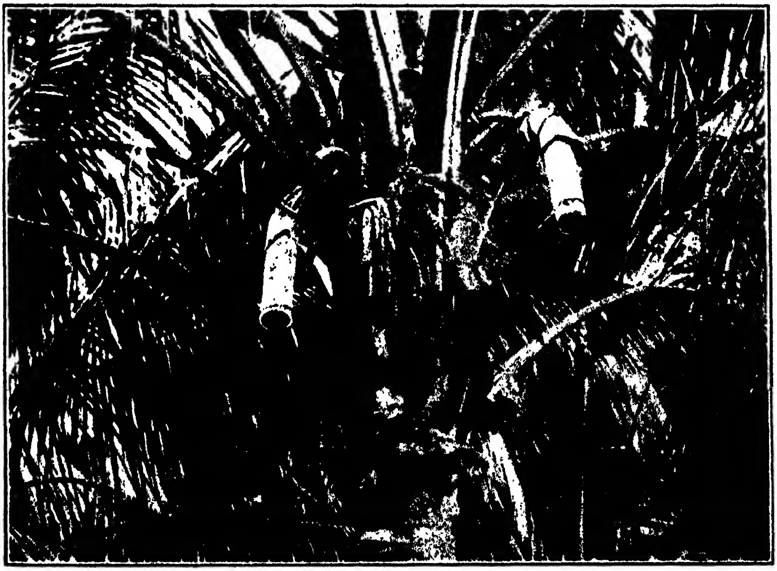


FIG. 156. Coconut palm with bamboo tubes, for collecting sweet sap, attached to inflorescence stalks

is cut across, it will be found, after sufficient time has elapsed, that the colored solution is inside the vessels. Water enters the outer cells of the roots, passes through the cortex into the stele, and enters the vessels. It then passes through the vessels of the root to those of the stem, and through these to the leaves, flowers, and fruits. The loss of water by transpiration from the chlorenchyma cells tends to increase the concentration of the contents of these cells. By osmosis and hydration of colloids the chlorenchyma cells draw water from the vessels, and so replace that which is lost through transpiration.

The mechanism by which the water moves up the vessels is in dispute. In the case of plants which reach great heights, in some cases one hundred meters or more, the source or application of energy to lift the water is one of the great puzzles to plant physiologists.

The ultimate source of energy may be sought in the radiant energy from the sun which is absorbed by the leaves and used to evaporate the water lost in transpiration. The energy used in evaporating the water is a great deal more than that called for to lift the water to the tops of the tallest trees. There is therefore no real puzzle as to the source of energy. The water is evaporated from the cells of the chlorenchyma into the intercellular spaces of the leaf. The chlorenchyma cells replace the water as it is evaporated by withdrawing water from the xylem of the veins and veinlets of the leaf. The energy to withdraw the water from the veins and veinlets is provided by the osmotic pressure existent in the chlorenchyma cells and increased by the evaporation of water in transpiration. As a matter of fact the pressures in these cells are in excess of that required to explain the height to which the water is lifted. The more significant and applicable fact is that the osmotic tensions are many times sufficient to withdraw water against any tension under which it is demonstrably present in the veins and veinlets.

It will suffice here to mention briefly theories which have been proposed to account for the rise of water in tall trees.

Root pressure. When plants are not actively transpiring and the stem is cut off near the root, water may exude from the cut stump. This water is forced out by turgor pressure in the root. However, when plants are transpiring actively there is no such exudation of water and, in fact, if water is placed on the cut stump of the tree it will enter the vessels. Root pressure may influence the upward movement of materials in a leafless stem in spring in temperate countries. Root pressure cannot, however, be invoked as an explanation of the movement of the transpiration stream, as it is not operative in the stem when transpiration is most active.

Capillarity. In fine tubes water will rise by surface tension to heights which depend upon the fineness of the tube. The vessels of plants are very fine tubes; not, however, fine enough so that the recognized physics of capillarity as applied to this problem seem to suffice to account for the lifting of water to any considerable fraction of the height to which it does ascend.

Atmospheric pressure. As water is lost by the leaf, the leaf by means of osmotic pressure draws water from the vessels, and so there is a tendency to produce a vacuum. It has been explained that atmospheric pressure acting on the water in the soil forces the water up the stem to replace that lost by evaporation. An objection to this theory is that the atmospheric pressure is not known to raise water more than about ten meters and there are trees which are a hundred meters or more in height.

Cohesion. The theory which has been most generally accepted is the cohesion theory. This theory is based on two factors which are generally accepted as facts. The first is that the osmotic force with which the leaves draw water from the vessel to replace that lost by transpiration is sufficient to lift the weight of the water which moves through the stem and also to overcome any resistance due to friction etc. The second is that in very small solid columns water holds together with great tenacity. In fact in capillary tubes a column of water will hold together with sufficient force so that a column as long as the height of the tallest tree could be lifted by a pull at the upper end. An objection which has been raised to the cohesion theory is that the water does not occur in the vessels as solid columns, because larger or smaller air bubbles are found in the vessels, and that water moves around these. It is argued that these air bubbles and also the movement of trees by the wind would cause the column to break. The claim is made, however, that solid columns of water have been demonstrated in small plants. While the cohesion theory is widely held, the objections to it have never been met satisfactorily enough to cause its universal acceptance.

Diffusion of water vapor. A very recent theory makes use of air bubbles in the vessels. This theory starts with the evident truth that all water in the plant is continuous, that in adjacent cells being continuous through the cell walls, that in vessels being continuous through the cell walls with that in surrounding cells, and so on throughout the whole plant. The water lining the vessels is thus continuous with that in all parts of the leaves and stems. Where a cell is deficient in water, water will be drawn from a neighboring cell to make good the deficiency. In turn, the cell which has given up water will again draw water from another cell. The cells in contact with vessels will draw water from them. That water is so drawn we know to be true. The rapid movement of water in the vessels of the stem is explained as being due to the movement of water in the form of water vapor. In an air bubble enclosed in a vessel with wet walls, there would be a tendency for the air bubble to be saturated with water vapor due to the evaporation of water from the wet walls. Gases diffuse rapidly, and so water in the form of water vapor should diffuse rapidly through an air bubble in the vessel. As water is drawn from one part of a vessel, there would be a tendency for this water to be replaced by the condensation of water vapor from the vessel, while the water which condenses would be replaced by evaporation from a more moist portion of the vessel.

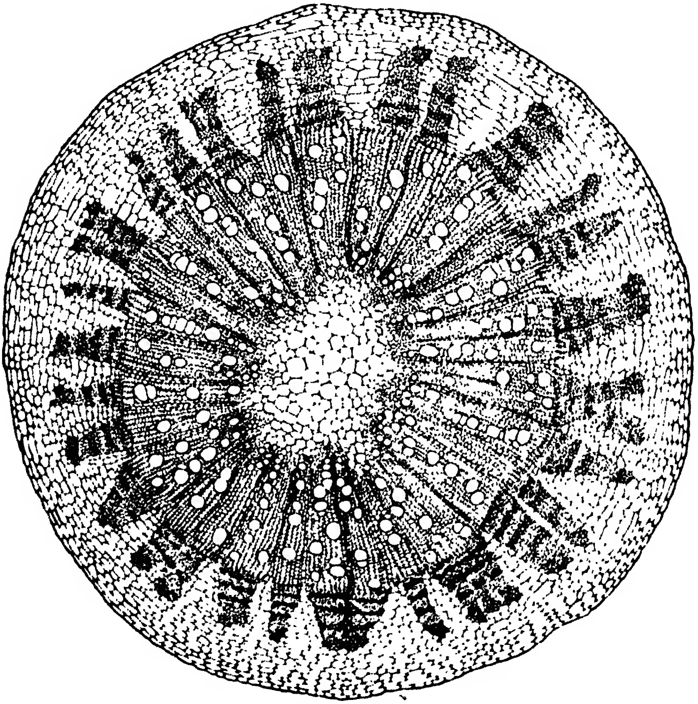


Fig. 157. A cross section of a young stem of a tropical tree, ylang-ylang (*Canangium odoratum*), in which there has been some secondary thickening

The wood is composed chiefly of wood fibers and large vessels. The bark has in the phloem an alternation of thin-walled cells and bast fibers. (× 40)

SECONDARY THICKENING

Formation of cambium. The vascular bundles of dicotyledons contain a single layer of cambium cells, which separates the xylem from the phloem (Fig. 126). While the other cells formed by the division of the meristem in the tip of the stem are being differentiated into permanent tissue this layer of cambium in the bundles remains meristematic. When the primary xylem and the primary phloem are first differentiated, there is no cambium across the pith rays to connect the edges of the cambium in the bundles. After the differentiation of the first xylem and phloem the cells of the pith rays, which lie between the edges of the cambium in the bundles, divide in a plane at right angles to the radial direction of the rays and form a layer of cambium across the pith rays. The beginning of this process is shown in Fig. 126. The newly formed cambium connects the cambium in the bundles, and this results in the formation of a continuous ring of cambium in the region between the xylem and the phloem (Fig. 157). In trees the region outside the cambium is known as *bark*,

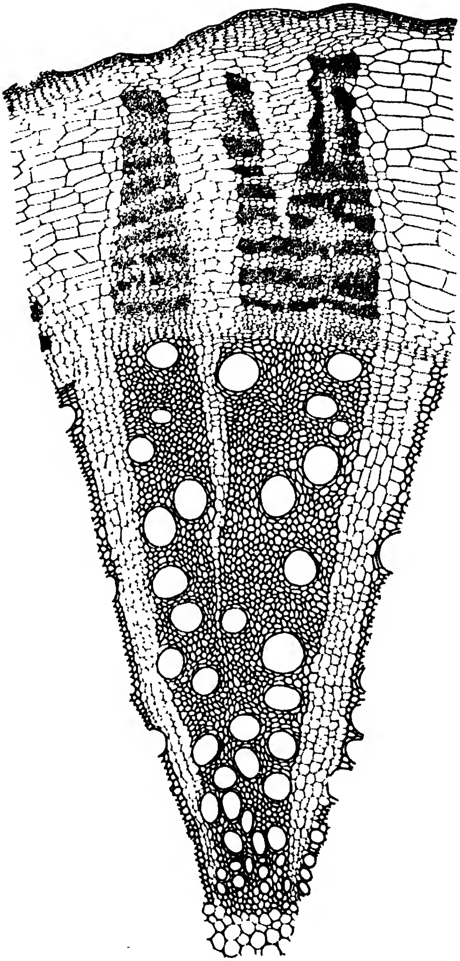


Fig. 158. A vascular bundle in a cross section of a portion of a young stem of a tropical tree (*Muntingia calabura*) which has undergone some secondary thickening

The xylem is composed largely of vessels and wood fibers. In the phloem region there is an alternation of bands of thick-walled bast fibers and thin-walled phloem cells. A secondary pith ray is shown in the center of the bundle. (× 70)

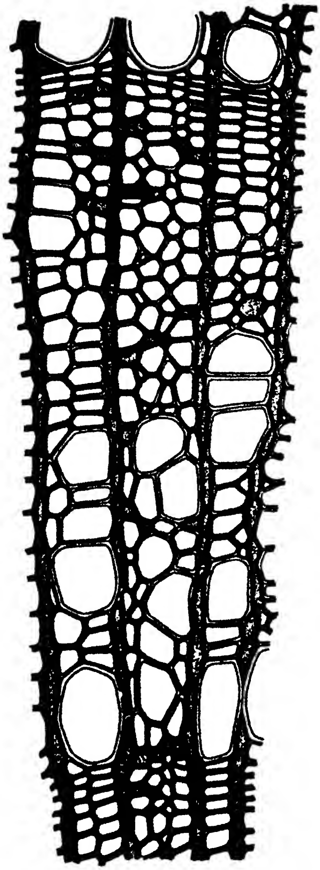


Fig. 159. Cross section of the secondary wood of a linden stem

Rows of cells extending from top to bottom, pith rays; large, thick-walled openings, vessels; smaller empty cells, wood fibers; small cells with gray contents, wood parenchyma. An annual ring ends with the small cells in the lower part of the drawing; another begins with the large vessels and ends near the top, just below the large vessels of the succeeding ring. (× 255)

while that inside is known as ***wood.*** Usually the bark can be readily separated from the wood, as the cambium cells are soft and weak and can be easily broken.

Activity of cambium. The cambium layer consists essentially of a single layer of cells. These cells divide in a direction parallel with the epidermis. Each time a cell of the cambium divides into two, one of the daughter cells remains meristematic, while the other is differentiated into permanent tissue. If the cell that is differentiated is next to the xylem it forms xylem, while if it is next to the phloem it becomes phloem. In this way new cells are added to the xylem and the phloem, and the bundles increase in size (Figs. 157, 158). While there is more or less alternation in the production of xylem and phloem cells from a cambium cell, more cells are formed on the xylem side than on the phloem side.

The cells formed from the cambium in the region of the pith rays become pith-ray cells. The activity of the cambium thus increases the length of the pith rays, so that the bundles and pith rays grow equally.

The formation of new cells from the cambium results in an enlargement of the stem that is known as the secondary thickening. The formation of new cells in secondary thickening continues throughout the life of the plant. It is in this way that the trunks of trees continue to grow in diameter.

After the cells which are to form xylem or phloem are cut off from the cambium, they undergo one or more tangential divisions before being differentiated into permanent tissue. In this way the cambium frequently comes to be bordered on both sides by cells which are very similar in appearance to cambium cells. The result is that on superficial observation the cambium appears to be several cells thick.

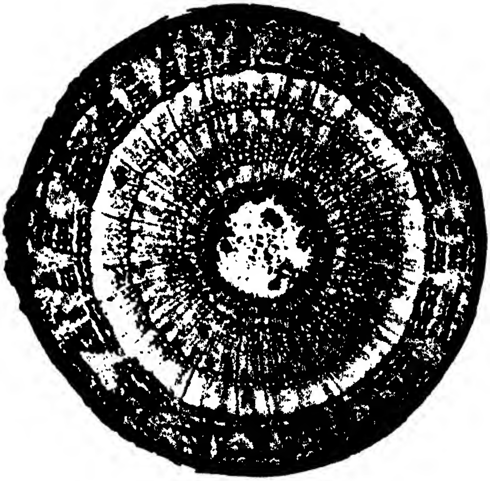


FIG. 160. Cross section of a three-year-old linden stem

In the center is the pith surrounded by three annual rings of wood. In the bark are alternating strands of phloem and bast fibers

Bast fibers. Very frequently there is in the secondary phloem an alternation of bands of thick-walled sclerenchyma fibers (known as bast fibers) and bands of thin-walled phloem cells (Figs. 157, 158). The bast fibers are like other sclerenchyma cells in being elongated, pointed, thick-walled dead cells whose function is to give strength to the group of tissues in which they occur. The term *bast fiber* is frequently used in a collective sense to denote the sclerenchyma fibers of the cortex, the pericycle, and the phloem. Strands of bast fibers have long been used by man for industrial purposes, having furnished early savages with bowstrings and material for cloth. Among the best-known commercial bast fibers are flax (from which linen cloth is made), hemp, jute (much used in making coarse sacks), and ramie (the so-called China grass).

Annual rings. In regions with a very pronounced cold season the diameter growth of woody plants takes place only during the

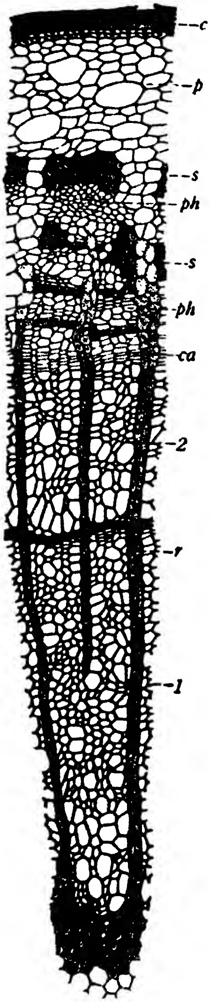


FIG. 161. Cross section of a portion of a two-year-old stem of tulip tree (*Liriodendron tulipifera*)

Near each side is a primary pith ray, while in the center is a secondary ray. 1, first annual ring of wood; 2, second annual ring of wood; *r*, pith ray; *ca*, cambium; *ph*, phloem; *s*, bast fibers; *p*, parenchyma; *c*, cork. (× 65)

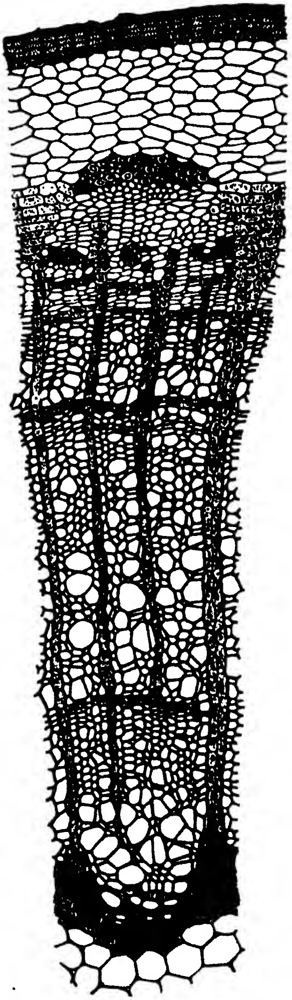


FIG. 162. Cross section of a portion of a three-year-old stem of tulip tree (*Liriodendron tulipifera*) with three annual rings of wood

Notice the primary, secondary, and tertiary pith rays. (× 75) spring and summer, and not in the winter. The wood of one season is sharply marked off from that of the next, because the wood formed first consists more largely of vessels than does that formed later, when wood fibers are relatively more abundant (Figs. 159, 160). In many trees vessels are formed only or largely in the first part of the season's growth. The production of the vessels early in the season is advantageous to trees in several respects, and is connected with their seasonal activities. In actively growing trees the number of leaves increases each year, and as all the foliage for a year is expanded during the early part of the growing season, additional vessels are needed at that time to supply the increased foliage. Moreover, the vessels in the leaves formed during one season are directly connected with the wood produced that same season; so for this reason also it is advantageous for the vessels to be formed as soon as possible, even when, as in trees past their prime, there is no increase in the number of leaves. In the case of coniferous trees similar conditions obtain, and the tracheids formed in the spring are much larger than those produced in the latter part of the growing season (Fig. 146). It is thus easy to distinguish the rings of wood formed in successive years in either dicotyledonous (Fig. 160) or coniferous trees of the temperate zones. These rings are called annual rings. The width of the annual rings varies with the environmental conditions at the

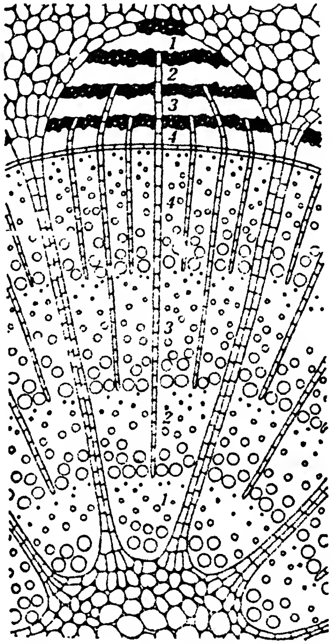


Fig. 163. Diagram of secondary thickening in a vascular bundle, showing four annual rings, labeled 1, 2, 3, and 4, in xylem and phloem

On both sides of the bundle pith rays run from the pith, while progressively shorter and shorter rays are found in the bundle. In the phloem region thick-walled sclerenchyma alternates with the phloem time of their formation; during favorable seasons wider rings are produced than during unfavorable seasons. As each ring represents a single season's growth, the age of a tree can be determined by counting the annual rings. Fig. 161 shows a section of a portion of a two-year-old stem with two rings, while Fig. 162 represents a portion of a stem with three narrower rings. Similar rings are sometimes produced in tropical countries where there is an alternation of pronounced wet and dry seasons; in this case the fundamental physiological factors involved are essentially similar to those which have been described. In most trees growing in tropical countries where there are no pronounced changes of season, there are no annual rings (Fig. 158).

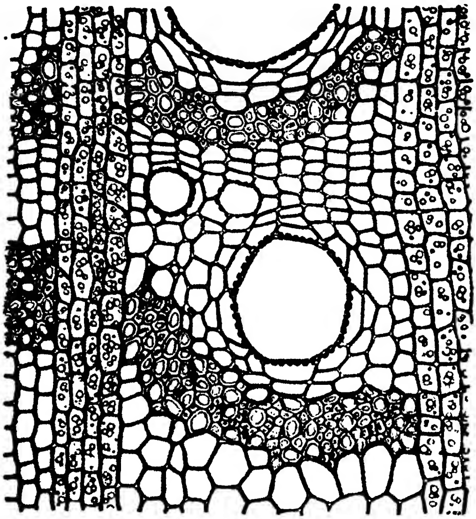


FIG. 164. Cross section of wood of coral tree (*Erythrina fusca*), a tree that has an unusually large amount of wood parenchyma and in which the wood parenchyma and wood fibers are exceptionally distinct

The rows of cells containing starch grains are pith rays, the small thick-walled cells are wood fibers, the small thin-walled cells between them are wood parenchyma, and the large openings are vessels. (× 85)

Secondary pith rays. As the course of the secondary thickening continues, the outer edges of the xylem and the inner edges of the phloem in the bundles naturally become wider and wider. They do not increase in width very greatly, however, before the cambium cells at the center of the bundle cease to form xylem and phloem but give rise to pith-ray cells. In this way new pith rays are formed in the bundles (Figs. 158, 161–163). As the secondary pith rays do not extend to the central pith or to the outer edge of the phloem, they are not as long as the primary rays. When the secondary thickening has progressed farther, tertiary pith rays make their appearance. They are naturally not as long as the secondary rays. In the same way, as thickening proceeds, other and progressively shorter pith rays are formed as is shown in Figs. 162 and 163.

The pith rays extend radially in the stem for considerable distances, the primary rays reaching from the pith into the bark; but the vertical extension is slight. The radial extension of the pith rays is of advantage, as they conduct food materials and water radially in the stem. A considerable vertical extension would offer no such advantage, but would result in weak places where the stem could be rather easily split. The vertical extension of pith rays is seen very readily in tangential sections. Tangential sections are longitudinal sections perpendicular to the pith rays (Fig. 165).

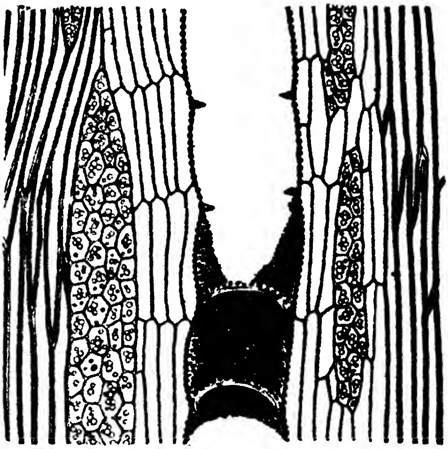


FIG. 165. Tangential section of wood of coral tree (*Erythrina fusca*)

A vessel is in the center, wood fibers with thick walls and pointed ends are at the sides, and the elongated blunt-ended cells are wood parenchyma. The groups of cells containing starch grains are pith rays. (× 75)

Heartwood and sapwood. The wood of large tree trunks consists of an outer region known as *sapwood* and an inner portion, the *heartwood*. The sapwood is usually light in color and from about a centimeter to several centimeters in thickness. In the sapwood the parenchyma cells are alive, and so it is in this portion of the wood that food is stored. Also, the ascending current of water moves in the sapwood, and not in the heartwood, which has practically no other function than that of mechanical support. The heartwood frequently has a darker color and is more resistant to decay than is the sapwood. Wood does not decay by itself, decay being due to the action of bacteria and fungi. The parenchyma cells of the heartwood are generally dead, but before they die they usually produce tannin, or some other antiseptic material, which permeates the walls of the neighboring cells. This antiseptic material makes the wood more resistant to the attacks of bacteria and fungi, and it is for this reason, and also because the heartwood contains less food material than the sapwood, that the heartwood is generally more resistant to decay and to the attacks of insects than is the sapwood. The dark color of the heartwood is also usually due to tannin, resins, or gums produced by the parenchyma cells.

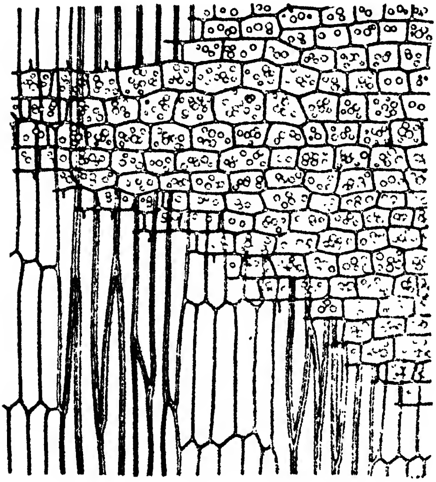


FIG. 166. Radial section of wood of coral tree (*Erythrina fusca*)

The wood fibers and wood parenchyma have the same characteristics as in the tangential section (Fig. 165). The group of cells containing starch grains is part of a pith ray. (× 95)

Weight of wood. The variation in the weight of woods is very great, as they contain varying quantities of air, but the wood substance itself has approximately the same weight in all species, being about 1.6 times as heavy as water. Therefore all woods would sink if they did not contain a considerable amount of air in the dead cells and intercellular spaces. When this air is removed, as after long submergence in water, the wood sinks. From the above it follows that the weight of a given wood will depend on its density, that is, on the relative proportion of wood material and air. The density and weight naturally vary with the number of wood fibers and the thickness of their walls. Wood that contains a great deal of parenchyma and few fibers is light (Fig. 164), while wood composed largely of thick-walled fibers is heavy.

Fuel value of wood. The fuel value of wood varies with its weight, as equal weights of wood produce equal quantities of heat. In general it may be said of woods otherwise equal that those light in weight kindle easily and flash quickly, the fire spreading rapidly, while those that are heavy behave in the opposite way.

The longitudinal arrangement of the fibers of wood explains why it is much easier to split it longitudinally than to cut across it. Wood splits most easily along the radii, on account of the radial arrangement of the pith rays.

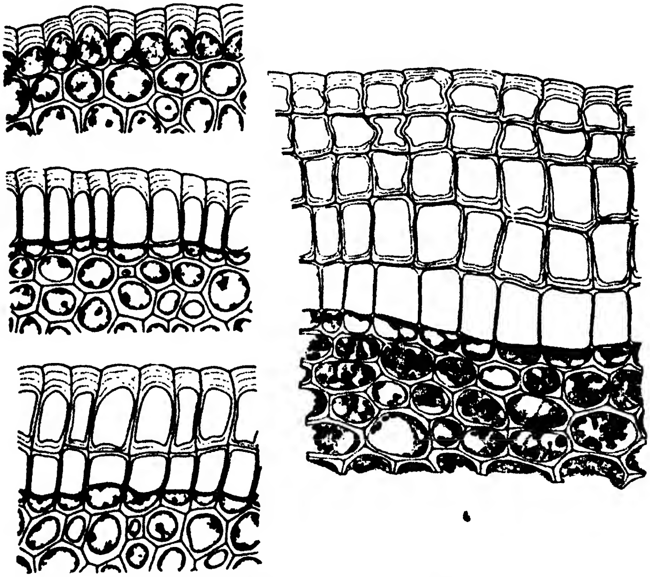


Fig. 167. Stages in the formation of cork of oleander (*Nerium oleander*)

Upper left, epidermis and outer part of cortex before the formation of a phellogen layer. Left center, the epidermal cells have elongated and divided to form a row of epidermal cells and below this the phellogen layer. Lower left, the phellogen layer has produced a single row of cork cells between the epidermis and the phellogen. Right, the uppermost row of cells is the epidermis, the next four rows are cork, while the sixth row from the top is phellogen. (× 250)

Wood pulp. Paper made from wood consists essentially of the fibrous elements, which are separated and then pressed together into sheets. In making paper from wood the fibers are separated, either by mechanical grinding or by boiling with chemicals. The loose fibrous material that is obtained in either of these ways is known as wood pulp. While wet, this pulp is combined with resin, clay, or other materials to give body and added strength, after which the pulp is pressed into paper.

Secondary changes in the bark. As the wood of the stem is enlarged by the cambial activity there is a tendency for the regions outside of the younger phloem to be stretched. This is partly compensated for by radial divisions of the parenchyma cells. When, however, there is a band of sclerenchyma, such as occurs in the pericycle of some stems (Fig. 126), the dead sclerenchyma cells cannot grow and divide, and can be stretched but little, if at all. Therefore as the wood increases in diameter the band of sclerenchyma is ruptured and parenchyma cells are pressed in between the isolated strands formed by the breaking up of this sclerenchyma ring.

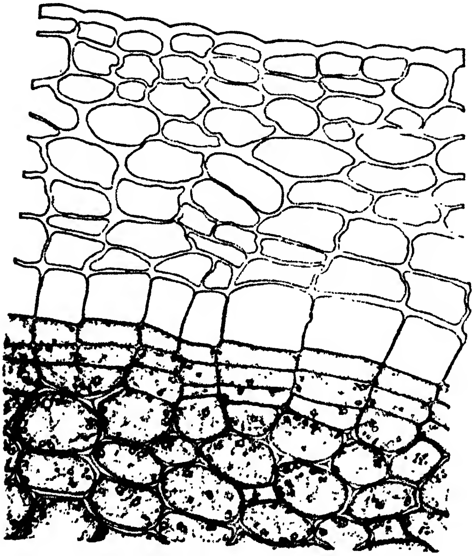


Fig. 168. Early stage of cork formation in *Ixora finlaysoniana*. (× 250)

The epidermis frequently increases in size by radial growth and division, but it seldom happens that the epidermis grows fast enough to prevent it from being ruptured by the increase in size of the tissues within it. If the place of the epidermis were not taken by some other protecting tissue, the cracking of the epidermis would expose the underlying tissue to an excessive rate of evaporation and would also allow the entrance of disease-producing organisms. These contingencies are prevented by the formation of cork.

Cork. Cork consists of dead cells which fit close together without intercellular spaces (Fig. 167). The walls of cork cells are impregnated with a waxy substance, suberin, which makes them practically impervious to water. Cork is familiar in the form of ordinary cork stoppers, which are obtained from the cork oak of Spain, on which cork is exceptionally well developed. Cork not only restricts transpiration but, like the epidermis which it replaces, hinders the entrance of parasites and affords mechanical protection.

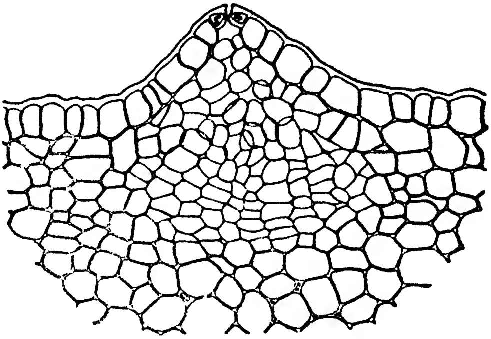


FIG. 169. Beginning of lenticel formation under a stoma of mulberry (*Morus alba*). (× 230)

Phellogen. The cork is formed from a layer of secondary meristem known as the *phellogen*. In a stem the first phellogen usually arises in the outermost layer of the cortex or in the epidermis (Fig. 167) by a tangential division of the cells, but it may have its origin in a deeper layer (Fig. 168). When the phellogen is formed by tangential division of the epidermis, the outer layer of cells remains epidermal, while the inner becomes the phellogen. When the outermost layer of the cortex by tangential division gives rise to the phellogen, it is the outer layer that becomes phellogen. As the phellogen is formed by the division of cells which had previously lost all the characteristics of meristematic cells, it is called second-

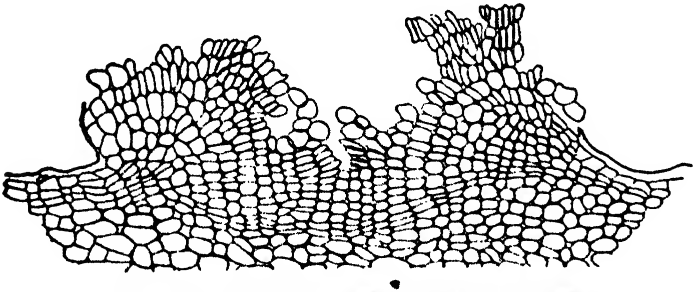


FIG. 170. Lenticel of mango (*Mangifera indica*)

Note the phellogen layer extending under the lenticel. (× 95) ary meristem. After the phellogen layer is formed, it divides tangentially and gives rise to radial rows of cork cells toward the exterior of the stem (Fig. 167), and frequently to parenchyma cells toward the interior. The cork cells soon become suberized and die. Also, the cutting off of the water supply of the cells that are exterior to the cork results in their death, and after a time they peel off and disappear.

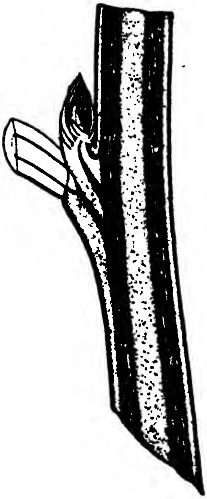


Fig. 171. Abscission layer at base of a mulberry leaf (*Morus alba*). (× 1)

The first-formed phellogen does not function indefinitely but is replaced by another produced in the underlying tissue. The second phellogen is likewise replaced by a third, and so on until the phellogen may come to be formed in the secondary phloem. As the older parts of the bark tend to peel off, the bark of old trees may consist only of secondary tissues, the cortex, pericycle, and primary phloem having been shed.

Lenticels. Stomata allow for an exchange of gases through an epidermis, and in the same way the lenticels allow for an exchange of gases through the cork. Lenticels are formed under the stomata (Fig. 169) and consist of radial rows of cells with intercellular spaces (Fig. 170). Like the cork cells, they are formed from the phellogen. The intercellular spaces allow for an exchange of gases.

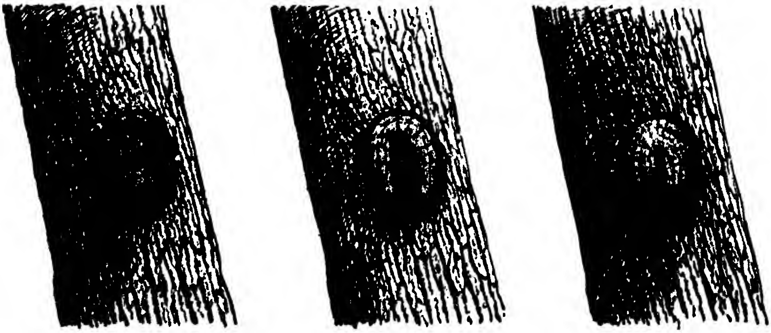


Fig. 172. Stages in healing of wound caused by removal of branch

Leaf fall. The fall of leaves is brought about by meristematic activity of cells across the base of the petiole. These produce layers of parenchyma cells which separate and cause the leaves to fall (Fig. 171). The scars are protected by lignification and suberization of the exposed cells and by the formation of a layer of cork continuous with that which covers the stem.

Healing of wounds. When a cut is made into the wood of a dicotyledon or a conifer, the cambium cells adjoining the wound area proliferate and produce what is known as a callus. This grows over the wound and covers it (Fig. 172). A phellogen layer is produced in the outer part of the callus, while a cambium, which is continuous with that in the stem, is formed in the interior. As the edges of the callus grow together over the wound the edges of the cambium also coalesce.

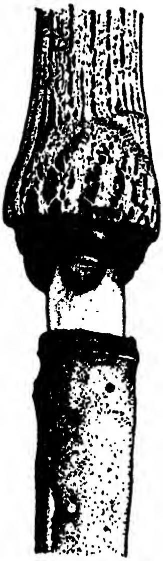


FIG. 173. A girdled tree trunk, showing greater growth above than below the wound

Removal of a strip of bark and cambium all the way around the trunk of a tree is called girdling. If the strip removed is sufficiently wide, the tree will be killed, because this operation destroys the food-conducting tissues which supply the roots. Some plants will recover from girdling if the strip removed is not too wide, as the wound may heal by the production of a callus and the subsequent formation of new conducting tissues. When a tree is girdled, the part of the trunk above the wound grows much faster and produces a much larger callus than that below it (Fig. 173), as the part above the wound

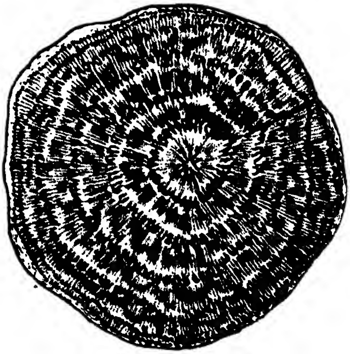


FIG. 174. Cross section of beet root showing concentric rings due to the presence of alternate rings of xylem and phloem

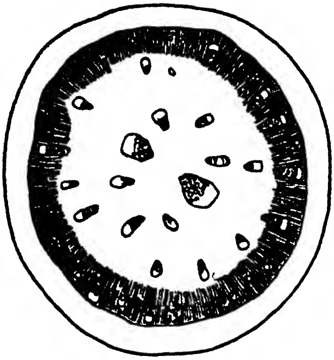


FIG. 175. Cross section of stem of four-o'clock showing ring of secondary wood formed exterior to the original vascular bundles. Diagrammatic, after De Bary

is abundantly supplied with food material, while the part below is not.

Anomalous secondary thickening. The method of secondary thickening just described applies to the majority of dicotyledonous plants, and the general features are characteristic of dicotyledons in general. There are, however, quite a number of plants which show variations. In the squash (Fig. 134) there is not only a cambium external to the xylem but also one internal to it.

An unusual method which is found in a number of plants is for the first-formed cambium to function for a while and then cease and be replaced by a new cambium formed in the pericycle. The second cambium may function for a time and then cease growth and may be followed by a third cambium formed in the phloem, and this by still another, etc. The concentric rings in the storage root of the common beet, which are often made conspicuous by the coloring of the root, are formed in this manner (Fig. 174).

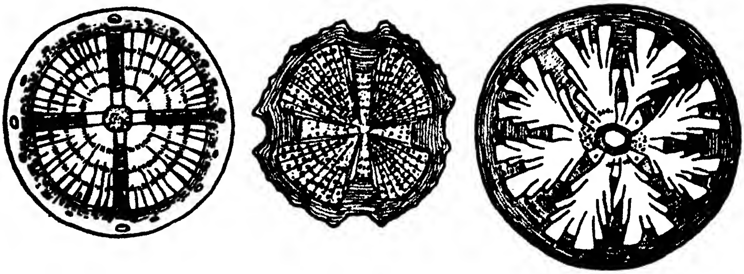


FIG. 176. Cross sections of stems of *Anisostichus capreolata*, *Pleonotoma* sp., and *Melloa populifolia* showing wood deeply cut up by phloem owing to slow growth of xylem and more rapid formation of phloem. In each figure the phloem is shown in concentric lines. Diagrammatic, after De Bary

In the four o'clock a continuous cambium ring is not formed between the first bundles which appear but around them and exterior to their phloem (Fig. 175).

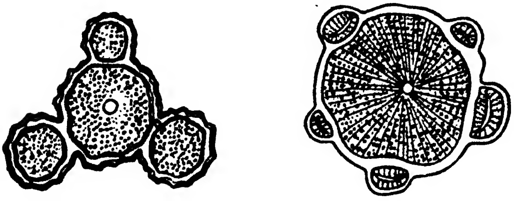


Fig. 177. Stems showing several rings of cambium. Diagrammatic, after Schleiden; from De Bary

Some vines which start out with a regular circular cambium show the strikingly peculiar anomaly that in certain places the development of wood proceeds slowly while phloem is formed rapidly, with the result that after secondary thickening has progressed for a time the wood is deeply cut up by masses of phloem which extend into it (Fig. 176).

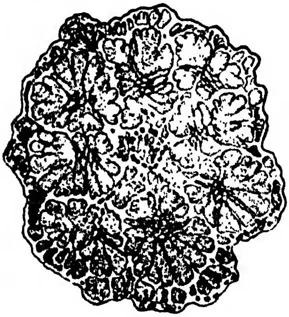


Fig. 178. Cross section of *Bauhinia* showing xylem broken up by growth of pith rays and parenchyma. Diagrammatic, after De Bary

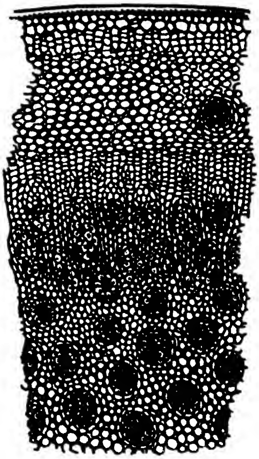


Fig. 179. Cross section of the outer part of a stem of *Dracaena* showing a meristematical cambium region between the vascular bundles and the cortex. Diagrammatic, after De Bary

In some plants there is a central ring of cambium producing secondary thickening, outside of which are other similar but usually smaller rings of cambium the activity of which also results in secondary thickening (Fig. 177).

A very bizarre effect is reached in some plants by the continuous growth of pith rays and parenchyma which split the xylem up into very curious shapes (Fig. 178).

Secondary thickening occurs in a few monocotyledons such as *Yucca*, *Cordyline*, and *Dracaena* (Figs. 179, 180). The arrangement of the stem produced by primary growth in such cases is much the same as in other monocotyledons. However, a cambium is formed in the parenchyma outside of the region of the vascular bundles. In the tissue developed on the inside of this cambium new vascular bundles appear, while the cells formed on the outside produce secondary cortex. Where this secondary thickening occurs in tree types, the cortex can be separated from the inner part of the stem in much the same way as a bark can be separated from the wood in dicotyledonous trees.

The development of secondary thickening in leaves may be rather similar to that of the stem but is much less extensive (Figs. 26, 181). Often the xylem, both primary and secondary, forms a crescent rather than a ring (Fig. 181).

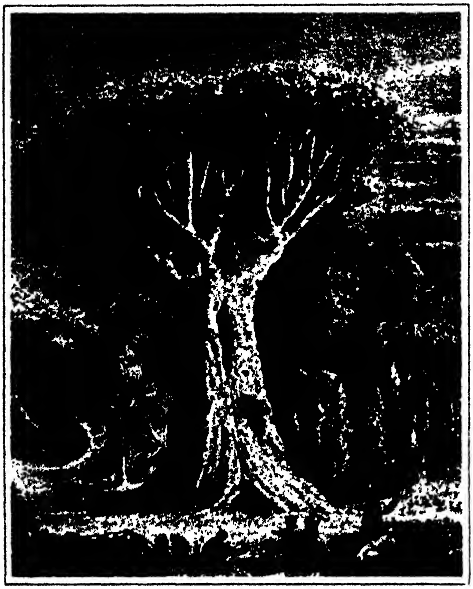


Fig. 180. An old tree, *Dracaena*, from Baillon

Pruning. In trimming a tree, branches should be cut off even with the trunk, and no portion of a dead or amputated branch should be left, if the wound is to heal properly. Stumps of branches are not in the direct line of the movement of food materials, and usually die quickly, if they do not send out new shoots. A callus formed from the main stem then starts to grow out over the stump, but before the stump is covered it begins to decay, as is clearly illustrated in Fig. 182. The decay extends into the wood of the main branch and trunk, with the result that the tree becomes hollow. For similar reasons, if a twig is to be cut back but not removed, the cut should be made a little above a bud and not in the middle or upper part of an internode. If a portion of an internode is left, it dies and its presence interferes with the closing of the callus over the wound.

Budding and grafting. Budding and grafting consist in inserting a part of one plant into another in such a way that a perma-

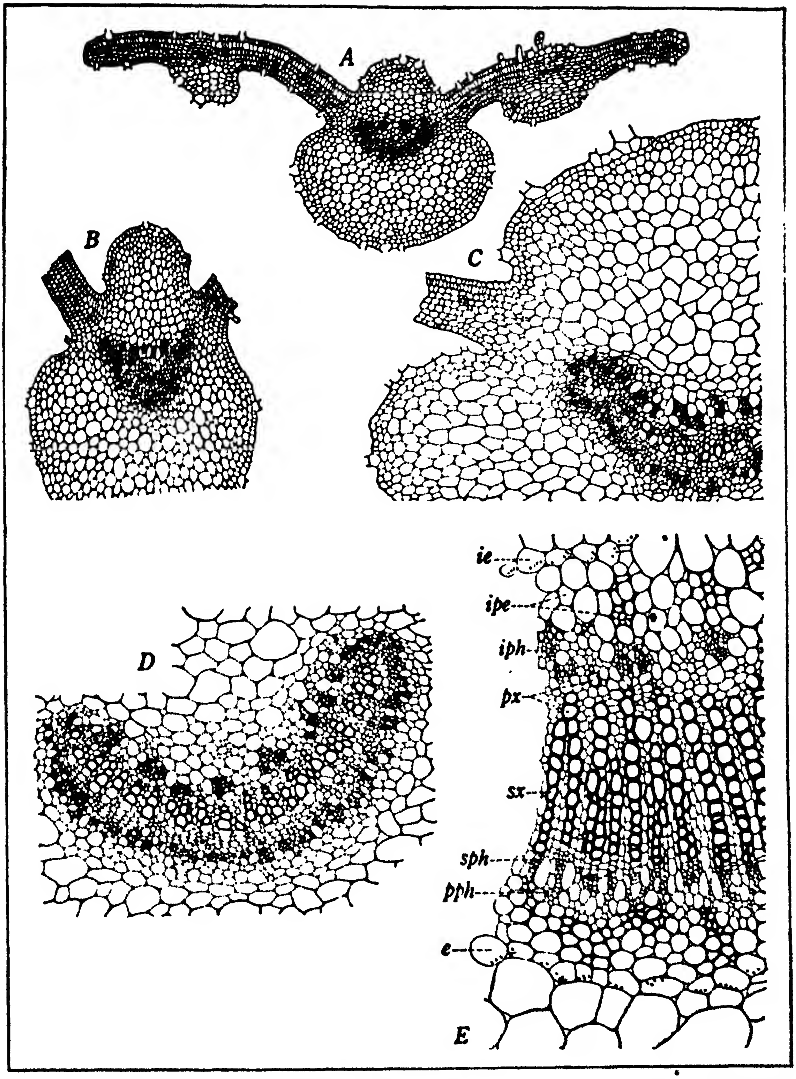


Fig. 181. Development of primary and secondary tissues in midrib of tobacco

A, cross section of a very young leaf showing midrib in the center; *B*, slightly older midrib; *C*, a still older midrib, showing primary xylem; *D*, vascular region of the midrib, showing cambium region between the xylem and the lower phloem; *E*, a portion of vascular region after there has been considerable secondary thickening: *ie*, internal endodermis; *ipe*, internal pericycle; *iph*, internal phloem; *px*, primary xylem; *sx*, secondary xylem; *sph*, secondary phloem; *pph*, primary phloem; *e*, external endodermis. (After Avery) nent union is formed and the inserted piece continues to grow. The part which is inserted is known as the *scion*, and the plant into which it is inserted is called the *stock*. The success of the operation depends primarily upon bringing the cambium of the scion into contact with that of the stock.

Budding consists essentially in removing a small piece of bark with a bud and little or no wood from one plant and inserting it under the bark of another plant (Fig. 183). The piece inserted is known as the *bud*. The usual method is called shield budding, on account of the shieldlike shape of the bud. In this method an oval piece of bark with a bud is cut from one twig. The stock is usually cut off above the place where the bud is to be inserted, while at the place of insertion a T-shaped slit is made through the bark into the cambium. The flaps are then loosened and the bud is inserted under them. The preparation is bound tightly to insure close contact of the inner surface of the bud with the cambium of the stock and to prevent the bud from getting out of place. The junction should then be very carefully sealed with grafting wax to prevent loss of moisture.

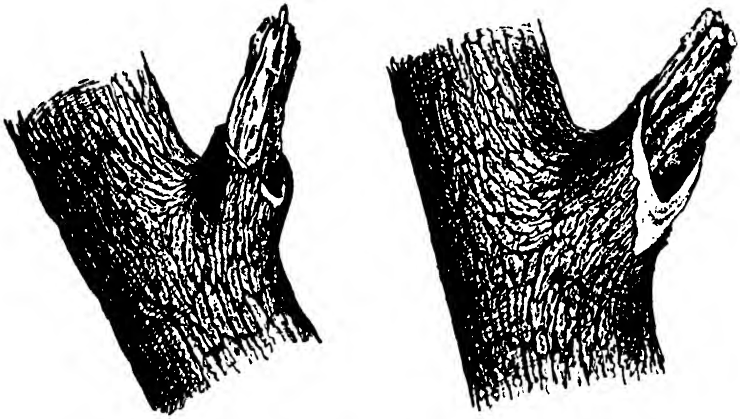


FIG. 182. Dead stumps, showing how decay may enter a tree trunk

Grafting consists in cutting off a piece of stem of one plant and inserting it into another. The common method of grafting when the stock is large is known as *cleft grafting* (Fig. 183). The scion consists of a small piece of twig with several buds. Its base is cut like a wedge. A vertical cleft is made into the decapitated stock and the scion inserted so that its cambium comes in contact with that of the stock. The wound is covered with wax to prevent drying. *Whip grafting* is employed on small stocks. In this method both stock and scion are cut obliquely and a vertical cleft is made in each. Stock and scion are then fitted into each other so that the cambiums are in contact. They are then tied together and the junction is sealed with wax.

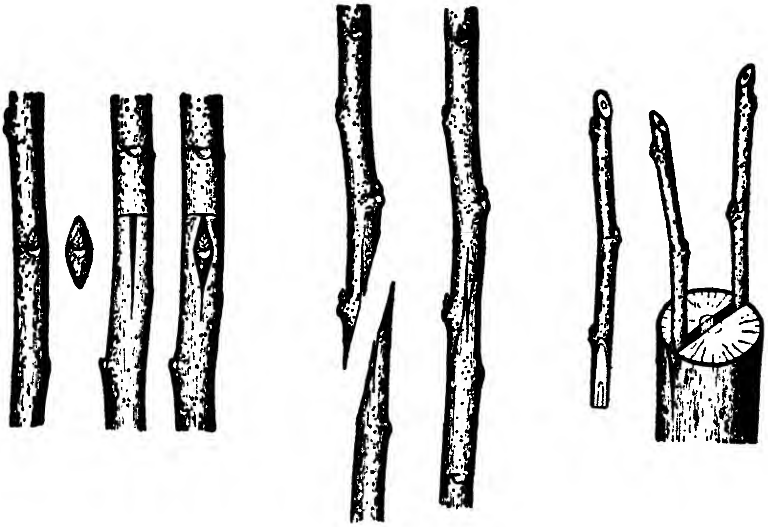


Fig. 183. Budding and grafting

Left, budding; center, whip grafting; right, cleft grafting

CHAPTER IX

GROWTH AND RESPONSES

GROWTH

The growth of a plant is usually accompanied by the addition of new material, but growth may consist in the rearrangement of materials already present. The latter is evidently the case when a potato or an onion sprouts in a dry, dark place, as under these conditions it is impossible for a plant to absorb water or mineral matter or to carry on photosynthesis. Growth in such cases is accompanied by an actual loss in weight, due to the breaking down of compounds in the process of respiration. This is necessary for the release of the energy used in the rearrangement of the materials taking part in the new growth.

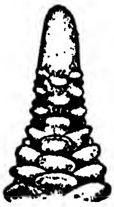


FIG. 184. Apex of stem of *Elodea canadensis*. Note naked tip and appearance and growth of leaf rudiments. After Caspary

Grand period of growth. If the formation and growth of a plant organ or a limited part of a plant are considered, it will be found that during its formation the rate of growth is slow. As it becomes older it grows more rapidly up to a certain period, and then more and more slowly until it is mature and growth ends. The total growing period is known as the *grand period of growth.* It can be divided arbitrarily into three stages, or phases, which necessarily overlap. The first is the phase of *formation,* during which the organ or other limited part of the plant has its initiation. The chief activity during this period consists in the multiplication of cells, and the rate of growth is relatively slow. Before the cells have ceased to divide, the part concerned enters into the next phase, that of *enlargement,* during which the cells enlarge and approach their mature size. This enlargement takes place with relative rapidity, and any part of a plant makes its most rapid growth while in this phase. After the cells have reached approximately their mature size, they enter the phase of *maturation*, during which they assume their mature characteristics. A part of a plant in this phase grows slowly, as the cells have, to a great extent, ceased enlarging.

EFFECT OF EXTERNAL FACTORS ON GROWTH

Water. An abundant supply of water is very essential to the most rapid growth of plants. It is a well-recognized fact that plants which lack water grow more slowly and produce smaller quantities of dry material than do plants that are abundantly supplied with water.

Any part of a plant, in order to grow, must contain enough water to be turgid. When cells or plant organs lose their turgidity, they decrease in size. Leaves, fruits, or stems may lose more water on a dry, sunny day than they absorb, and actually become smaller than they were during the preceding night. It is therefore necessary for normal growth that a plant should be able to obtain not only enough water to replace that which is lost through transpiration and that which is used in photosynthesis but, in addition, enough to fill the newly formed tissue. The amount needed for growth is very small as compared with that lost through transpiration.

The actual rate of transpiration is not so important as is the ratio between water lost and water absorbed. It is highly important that the daily rates of transpiration and of water absorption should be so balanced that the water absorbed is sufficient to replace that lost by transpiration and to support new growth. Excess of water loss over water absorption may be brought about either by a high rate of evaporation or by a low moisture content of the soil, or by a combination of these two. This condition can usually be remedied by either decreasing the rate of evaporation or increasing the water content of the soil. In agriculture the method most generally practiced is to supply water, as by irrigation.

Heat. At very low temperatures plants do not grow. The minimum, or lowest, temperature at which a plant will grow varies with different species, but 4° C. may be regarded as an average minimum temperature for many plants. As the temperature increases beyond the minimum the rate of growth becomes more rapid until the optimum temperature is reached. This optimum temperature also varies with different species, but probably averages from 28° to 30° C. If the temperature rises beyond the optimum, the rate of growth decreases until a temperature is reached above which no growth takes place. This temperature is known as the maximum. The minimum and optimum temperatures for growth vary not only with different species but also with changes in other environmental conditions.

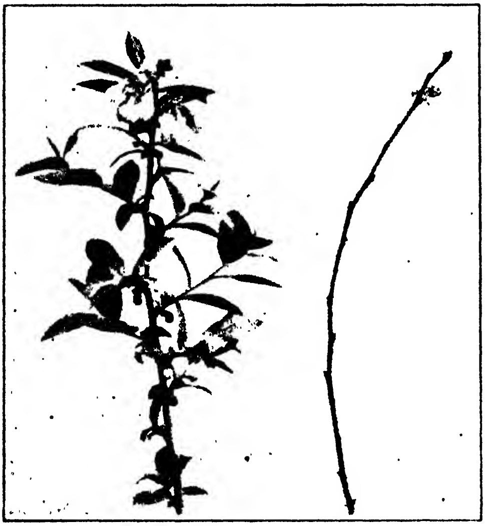


Fig. 185. Photographs of blueberry twigs, both taken in the spring at the same time

The one on the left had been exposed to a cold winter while the other had been kept warm in a greenhouse. (After Coville)

The effect of temperature is not confined to the direct action of favorable or unfavorable temperature on the rate of growth. Thus, trees from the temperate zone do not thrive in the tropics, where the temperatures are favorable to growth throughout the year. Trees which are native to the temperate zone seem to need a winter season, while tropical ones do not.

Trees and shrubs of the temperate zone, which are usually dormant during the long winter, tend to become dormant in the tropics after a period of activity. Unless they are exposed to an extensive period of cold though not necessarily freezing weather, the resumption of growth is greatly delayed, while the growth is lacking in vigor (Fig. 185). It is probably for this reason that such fruits of the temperate zone as apples, pears, peaches, and cherries do not thrive in the tropics. They grow well for a time and then become half dormant and, in the absence of chilling, never fully recover from this condition.

The advantages of chilling for trees of the temperate zone seem to be connected with changes in the character of the stored food. During the summer and autumn food is stored in the form of starch, which is insoluble. Before this can be used for growth it must be changed to sugar, which is soluble, and in these plants this change appears to take place most readily at low temperatures.

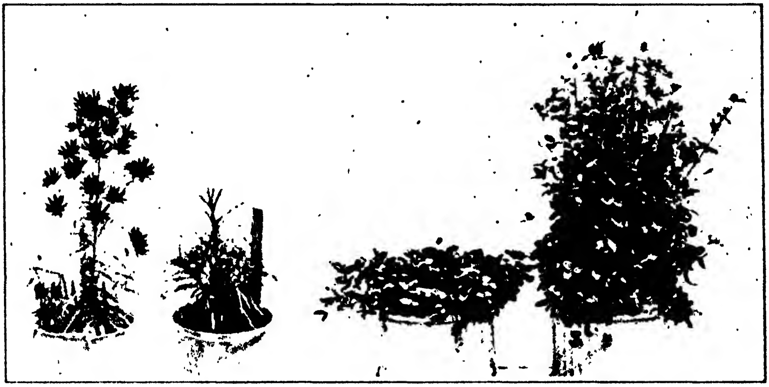


FIG. 186. Effect of lengths of day on different types of plants

Left, *Helianthus angustifolius*, a "short-day plant." Both specimens planted March 2 and photographed July 31. Plant at left kept in the dark during a portion of each day and exposed to light for only ten hours. Plant at right exposed to light for full length of day. Right, red clover, a "long-day plant," photographed June 28. Plants at left kept in the dark during a portion of each day and exposed to light for only ten hours. They assumed a prostrate form of growth and were greatly delayed in flowering. Plants at right exposed to light for full length of day during spring and early summer. (From work of Garner and Allard, Bureau of Plant Industry, United States Department of Agriculture)

Trees of the temperate zone are afforded valuable protection by the fact that in the fall they enter into a condition of dormancy from which they do not emerge until exposed to prolonged chilling. If such plants were so constituted as to start into growth as easily in the warm days of late fall as they do in early spring, many species would come into flower and leaf in warm autumn days which follow cold ones, and the stored food that they require for their normal vigorous growth in the following spring would be wasted in the growth of new twigs which would be killed by the first heavy freeze. These evil results are prevented when two or three months of chilling are necessary before a dormant plant will respond to a favorable temperature by the resumption of growth.

Light. As the growth of green plants is dependent on photosynthesis, plants cannot continue to grow for any great length of time without light. On the other hand, high intensities of light are usually accompanied by rapid rates of evaporation. In the preceding chapter it was pointed out that plants may contain less water on sunny days than on cloudy days or during the night. This condition frequently results in a much more rapid rate of growth during the night than during the day, and plants may even cease growing or actually shrink during bright, dry days.

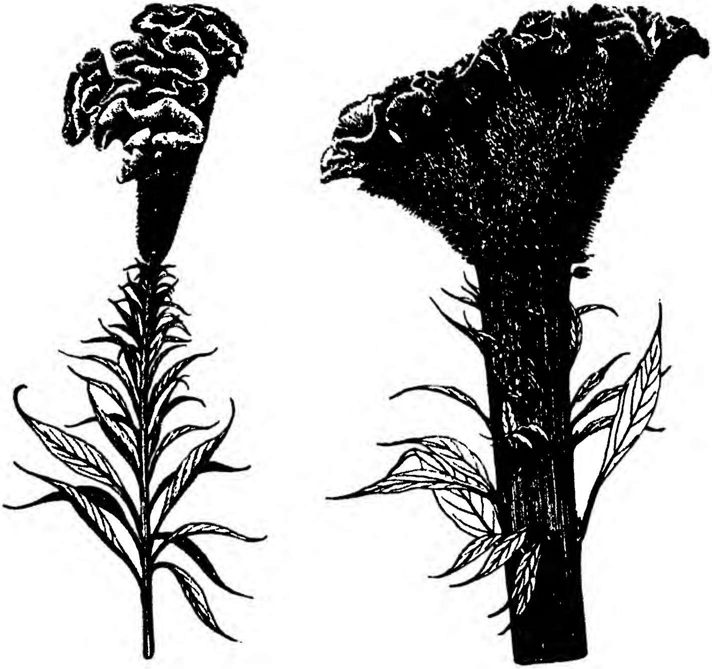


FIG. 187. Two views of the same fasciated stem of cockscomb

The relative length of day and night is a very important factor in determining the fruiting season of plants. Some plants, as *Poinsettia* (Fig. 98), will flower and fruit only during seasons with short days, and others only when the days are long. In temperate zones the days are long during the summer, shorter in autumn, and still shorter in winter. It has been found that many plants which normally do not flower until the short days of autumn can be made to bloom during the long days of summer if they are placed in the dark for a portion of each day (Fig. 186). Also, many plants that usually blossom in the summer, and not in the winter even if in a heated greenhouse, will produce flowers during the short days of winter if kept in a warm greenhouse and illuminated by electric lights for a portion of each night.

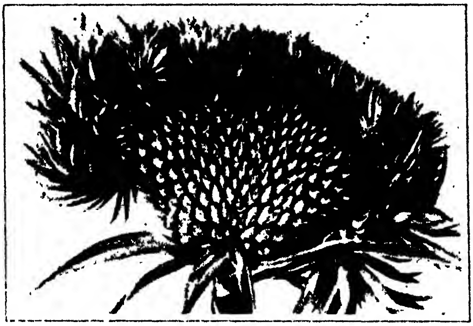


Fig. 188. Fasciated fruit of pineapple. The pineapple is really a stem bearing many fruits fused together. Fasciation of this type is not unusual. Compare Fig. 330

While the period of flowering may be hastened by shortening the daily exposure to light, the rate of growth frequently increases with the length of the daily exposure. When plants which germinate in the spring and flower in the fall are forced into bloom early in the summer by shortening the daily exposure to light, they are small at the time of flowering.

In the tropics the days are always shorter than the summer days of temperate zones. Plants from the tropics may fail to flower during the long days of northern summers and

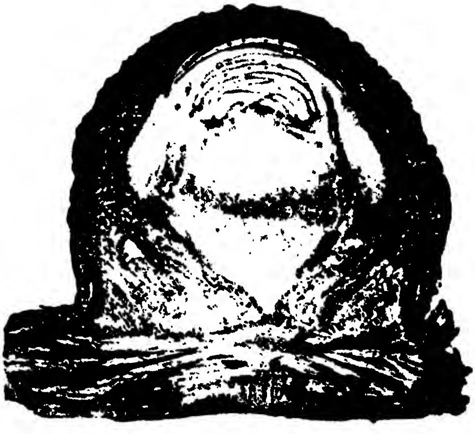


Fig. 189. Section of a gall on a *Cissus* root in which a bud of *Rafflesia manillana* is developing

Later the bud will burst through the gall. Compare with Fig. 7

produce flowers and fruits abundantly in greenhouses during the shorter days of winter.

The fact that the days are shorter in the tropics than they are during the summer in temperate zones may explain why many of the plants of the temperate zone do not succeed in the tropics.

Abnormal forms of growth. Stems and other plant organs frequently show abnormal growths. One of the most common is a flattened form, called fasciation, which occurs when a stem has several growing points instead of a single one. This abnormality may be inherited, as in the cockscomb (Fig. 187), or it may be due to an injury, as by insects (Fig. 188). Galls are another common class of abnormality. They may be produced by parasitic bacteria, fungi, flowering plants (Fig. 189), or various classes of animals, especially insects. Insect galls are very numerous, those produced by a given insect on the same kind of plant being constant in form. The mother insect lays its eggs in the host plant; and after the eggs hatch, the tissues of the plant proliferate and produce the galls.

RESPONSE OF STEMS AND LEAVES TO EXTERNAL CONDITIONS

Geotropism. It is a very common observation that stems grow upward and roots downward. Even in the case of most prostrate stems the tips tend to grow upward. This tendency of stems to grow upward and roots to grow downward is due to the force of gravity. Such responses of a plant to gravity are known as geotropism. When roots grow downward, or in the direction of the force of gravity, they are said to show *positive geotropism,* while stems that grow upward against the force of gravity exhibit *negative geotropism.*

The action of geotropism can be demonstrated very easily if we take a small seedling and lay it in a horizontal position. The stem will bend upward, while the root will turn downward. The stem and root will then continue to grow in these directions. If, however, we place a seedling in a horizontal position and revolve it around its own axis, so that all sides shall be subjected in the same way to the force of gravity, then the stem and root will continue to grow in a horizontal direction. The action of the negative geotropism of stems is clearly seen in the case of plants which have been blown over but continue to grow. In such cases the stems grow upward, away from the surface of the earth.

The action of geotropism is not due to a direct pull of gravity on the plant but is a response of the plant itself, as is shown by the fact that stems grow upward against the pull of gravity, while roots may exert considerable force in growing downward; in fact, roots must exert force to penetrate the ground. The difference in reaction of stems and roots is not the result of any difference in the force of gravity on the parts concerned but is caused by differences inherent in the organs themselves. The response to gravity is brought about by different rates of growth on the upper and lower sides of the organs concerned, the side which becomes convex growing more rapidly than the opposite side. Geotropism is largely responsible for the position of upright stems. Branches do not show the action of geotropism to the same extent as does the main axis.

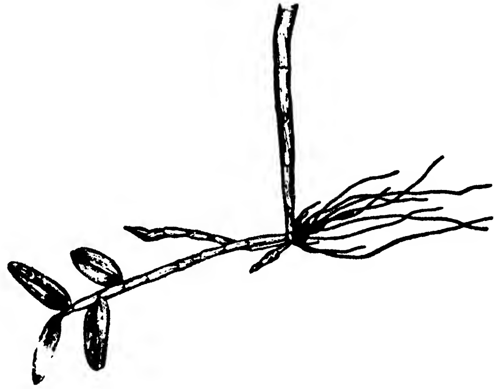


FIG. 190. The tip of a pendent stem of an orchid (*Dendrobium anosmum*) (see Fig. 2) producing a young plant

The parent plant hangs under the edge of a porch; the new shoots are growing toward the light, and the roots away from the light. (× ¼)

Phototropism. Stems tend to grow toward the light, while most aerial roots grow away from the light (Fig. 190). The tendency of plant organs to orient themselves with reference to light is called phototropism. An organ that grows toward the light exhibits *positive phototropism*, while an organ that grows away from the light shows *negative phototropism*. Nearly all roots that normally grow in the ground show little or no phototropism; but there are some exceptions, as in the case of the radish, where the roots are negatively phototropic (Fig. 191).

The effect of phototropism can often be clearly seen in upright plants growing very near a house. In such cases there is a tendency for the branches to grow away from the house, or, in other words, toward the source of greatest illumination. There is also a tendency for the main stem to lean away from the house, or toward the light. In trees that bend toward the light the position of the main axis is very clearly the result of the combined action of geotropism and phototropism: the general upright position of the stem is due to geotropism, while the leaning position is the result of phototropism. The effects of phototropism are frequently pronounced in plants growing in windows or on covered porches. In such cases the plants usually lean toward the source of light (Fig. 192).

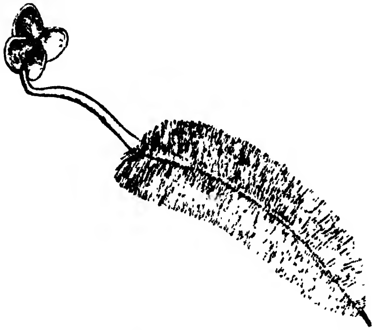


FIG. 191. A radish seedling grown on the side of a piece of blotting paper held vertically in a darkened box with light entering on the left side

The position of the shoot is due to a combination of positive phototropism and negative geotropism; that of the root, to negative phototropism and positive geotropism. (× 1)

The tips of herbaceous stems frequently follow the course of the sun during the day, pointing to the east in the morning and to the west in the afternoon. This is true of the sunflower.

Diaphototropism. Leaves usually turn to face the source of greatest illumination, and also bend in such a way that they are not greatly shaded by the leaves above them. The turning and bending of leaves to face the light is called diaphototropism.

When leaves have petioles, the bending takes place in the petioles. If the petioles on pendent branches were straight, the morphologically upper side of the leaves would face downward, but in such cases the petioles bend and twist so as to expose this side to the strongest light (Fig. 193). In many cases the bending and twisting of the petioles or the twisting of the stem is much more important than the place of attachment of the leaves in determining the position of the leaf blades. This is often very clearly

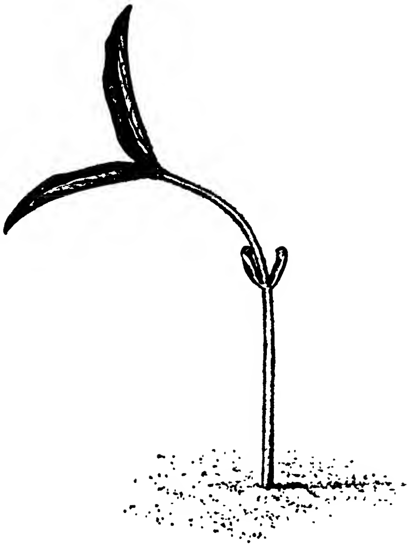


Fig. 192. A mungo bean seedling which grew upright when illuminated from all sides and then bent toward the light when illuminated only from the left. (× ½)

seen in the different positions of leaves on vertical and horizontal stems of the same plant. On vertical stems which are not shaded on one side the leaves extend straight out from the point of attachment, while if the illumination is one-sided, as upon unshaded horizontal branches, the stems or petioles frequently bend and twist so as to bring the blades into such a position that they face the strongest light. Compare Fig. 111 with Fig. 116, and Fig. 195 with Fig. 194. On horizontal branches the leaves are often arranged in an approximately horizontal position. As an example take the case of a plant on which the leaves are arranged in five vertical rows. On a vertical stem the leaves will extend from the stem in five directions (Fig. 194). On a horizontal branch of the same plant the petioles will bend and twist so as to bring the blades into an approximately horizontal position, and the leaves will appear to grow from only two sides of the stem (Fig. 195).

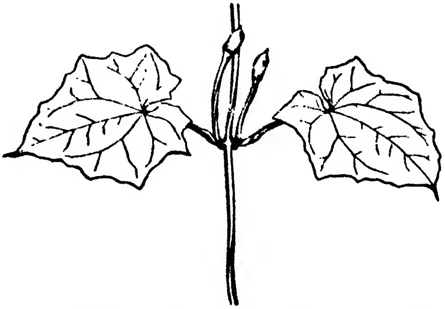


Fig. 193. Leaves of *Thunbergia grandiflora* on pendent branch

The petioles have twisted so that the morphologically upper sides of the leaves are uppermost. (× ¼)

The degree of adjustment of leaves in response to light varies greatly in different plants. Leaves

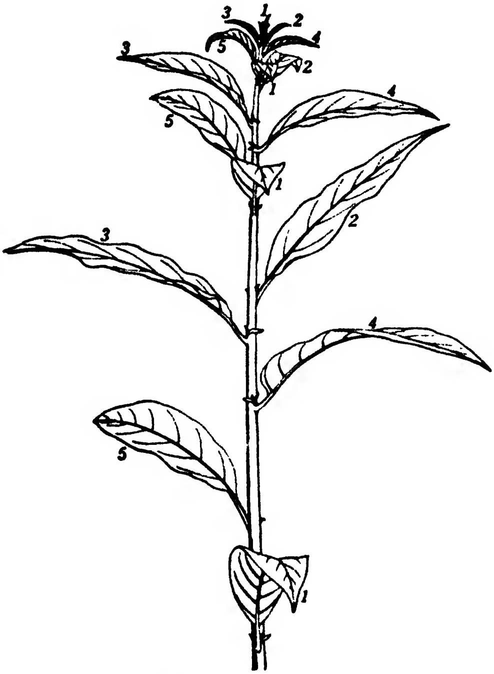


Fig. 194. Vertical branch of *Cestrum nocturnum* illuminated from all sides

Compare with Fig. 195. (× ⅓)

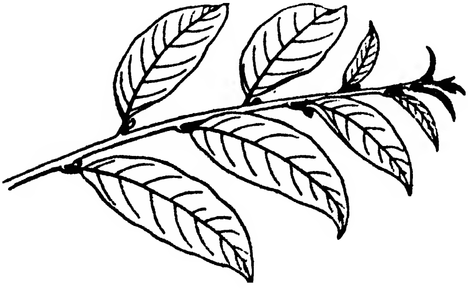


Fig. 195. Arrangement of leaves on horizontal branch of *Cestrum nocturnum*; position of leaves due to one-sided illumination

Compare with Fig. 194. (× ⅓)

which are very sensitive to light follow the course of the sun during the day; leaves which are only moderately sensitive usually face the strongest light, as is the case with most common trees and shrubs; while leaves which are feebly sensitive are not so definitely arranged.

Hormones. The causes of geotropic and phototropic responses have been investigated most thoroughly in roots and in coleoptiles, which are the sheaths that cover the apexes of the seedling shoots of grass. In coleoptiles it is the tip that is sensitive to light, while curvature occurs at the base. There is thus a region of perception of the stimulus at the tip which is separated from the region of response at the base. In roots it is the tip that is sensitive to geotropic stimulus, while curvature occurs back from the tip. Here also there is a sensitive region separated from the region of response.

In the stimulated tips of coleoptiles and roots there is formed a growth-regulating substance or hormone, and it is the diffusion of this hormone toward the responding region that results in the unequal growth which produces curvature. Internal secretions or hormones are numerous and important in animals. The growth-regulating effect of thyroid secretions is well known. In animals the hormones are distributed in the blood stream; the growth-regulating hormone responsible for heliotropic or geotropic curvature in plants travels by diffusion.

The existence and diffusion of a growth-regulating hormone has been demonstrated in several ways. The tip of a coleoptile or root can be cut off and separated from the remainder of the coleoptile or root by gelatin, when the hormone diffuses through the gelatin to the stump of the coleoptile or root and produces curvature. If a sheet of tin foil is placed between the tip and the remainder of the coleoptile or root no response results.

An even clearer demonstration can be made by placing severed coleoptiles or root tips on a small block of gelatin, and allowing the growth-regulating hormone to diffuse into the gelatin. The block of gelatin can then be placed on the end of an unstimulated coleoptile or root from which the tip has been removed. The growth-regulating hormone will then diffuse into the coleoptile or root and cause curvature.

There is an indication that only one growth-regulating hormone is concerned, as the tip of a coleoptile which has been stimulated can be cut off and placed on the end of a root from which the tip has been removed and cause curvature. Likewise, a root tip can cause curvature in a coleoptile. Moreover, the growth-regulating hormone from a coleoptile can be allowed to diffuse into a block of gelatin and this block of gelatin will cause response when placed on the end of a root from which the tip has been removed. Likewise, a gelatin block into which the hormone has diffused from an stimulated root tip will cause curvature in a coleoptile.

In the developing shoots of many plants, the buds in the axils of the leaves remain dormant as long as the apex of the shoot is growing but develop into branches when the apex is removed. It has been found in some cases investigated that the failure of the lateral buds to develop while the apex is growing is due to the action of a growth-inhibiting hormone formed in a few of the very small developing leaves but not in the very small leaf rudiments.

Unusual positions of leaves. While the leaves of most plants are in general arranged so that they face the source of greatest illumination, there are some exceptions. The leaves of many plants, particularly of those growing in arid regions, make acute angles with the rays of light from the source of greatest illumination. This arrangement has certain advantages. Very intense light has a tendency to destroy chlorophyll. It also has a tendency to heat the leaves excessively and to produce rapid transpiration. These injurious effects are partly avoided by plants that have their leaves arranged in the manner just described.

Leaf mosaics. The petioles of old leaves are usually longer than those of younger leaves on the same branch. In many plants the bending and twisting of the petioles, or a combination of these movements with different lengths of the petioles, brings all the blades into approximately the same plane and in such a position that they fit in between each other with very little overlapping. Such an arrangement of the blades is called a leaf mosaic, from the similarity to the fitting in of materials in mosaic work.

Heliotropism. The term *heliotropism* is often used in place of the word *phototropism.* Heliotropism is the orientation of plant organs in response to sunlight. Stems and leaves, however, respond to artificial light as well as to sunlight, so that it is better to use the general term, *phototropism,* than the specific one, *heliotropism.*

Etiolation. Stems that grow in the dark have a tendency to grow longer and to be more slender than those that develop in the light. They also have a blanched appearance, due to a lack of chlorophyll. The leaves of plants grown in the dark are usually small and also have a blanched appearance. Plants that have stems and leaves with these characteristics, which are the result of growth in the dark, are said to be etiolated. Etiolation is well illustrated in Fig. 196. A practical use is made of etiolation in China and Japan, where young sprouts of bamboo are used for food. These are made white and tender by covering them with earth or earthenware jars. Similar results are achieved with asparagus by cutting the shoots when the tops are just aboveground.

In nature, when upright stems grow in the dark they usually arise from underground structures such as bulbs or rhizomes, or are produced by germinating seeds. In such cases the relatively longer, slender structure of etiolated stems has a tendency to make the plants reach up into the light. The production of small leaves on etiolated stems also seems to be of advantage, as leaves in the dark cannot carry on photosynthesis and so are of no particular use to the plant. Moreover, large leaves would hinder the growth of stems through the ground, while their formation would require material which could be used in elongating the stem.

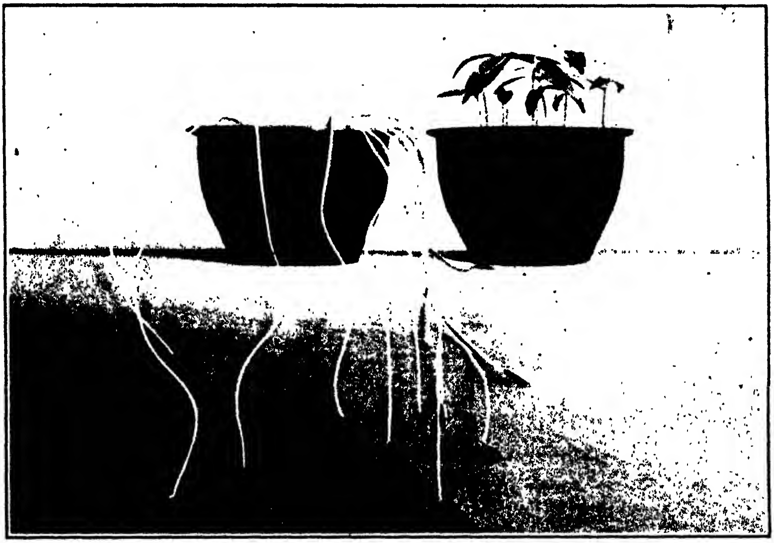


Fig. 196. Etiolated seedlings (left) and normal seedlings (right) of mungo bean (*Phaseolus radiatus*)

Leaves that normally arise directly from underground structures behave differently from ordinary aerial leaves when grown in the dark. Instead of being smaller than usual they become longer. This has the same effect as the elongated growth of upright stems in that there is a tendency to bring the leaves into the light.

Self-pruning. The heavily shaded portions of branches frequently shed their leaves, while whole branches that are heavily shaded usually die and fall from the plant. It is for this reason that the leaves of trees are usually found near the circumference of the crown and not in the interior.

The loss of shaded branches can be seen very plainly in the case of trees which grow close together and produce long trunks. As the lower branches become heavily shaded they die and fall from the tree, and leave the lower part of the trunk clear of branches. It is a common observation that trees growing close together are tall and slender in form and have long, clear trunks, while a tree growing in the open, where it is not shaded, usually has a spreading crown and a short trunk. These differences are due to the fact that if trees grow close together the lower portions are shaded and the lower branches die, which is not the case with trees which develop in the open. The dying and falling of shaded branches is called self-pruning. Foresters take advantage of the self-pruning of trees, and plant seedlings close together so that long, clear trunks will be produced. If it is desired that a tree growing in the open shall have a long, clear trunk, it frequently becomes necessary to remove the lower branches.

CHAPTER X

SPECIALIZED STEMS

The chief function of ordinary stems is to support the leaves and reproductive organs in such a way that they can carry on their several functions advantageously. Many stems, however, are specialized for functions which are unusual for stems, or are fitted to perform the usual functions in a somewhat specialized manner. Stems of these types may be called specialized stems. They may be divided into the following general classes: *unusual methods of support* (stem function), *photosynthesis* (leaf function), *absorption* (root function), *reproduction* (seed function), *storage*, and *protection.* This list is very similar to that given for specialized leaves. Frequently the only way in which we can tell by superficial examination whether a given structure is a stem or a leaf is by the mode of its attachment. If the structure is in the axil of a leaf we regard it as a stem, while if a stem or bud is found in its axil it is considered a leaf.

Unusual methods of support (stem function). Stems that are specialized in no other way than to support the leaves and reproductive organs in a rather unusual manner are well exemplified in climbing plants. The chief advantage of the climbing habit seems to be that it enables a plant to reach up into the light and bear large numbers of leaves without the necessity of expending the material which would be necessary to build a stem sufficiently strong to support the leaves and reproductive organs by its own strength. A climbing plant depends on the strength of some other object for its support, and so can develop long, slender stems. It is probably because of their slender stems that climbers usually grow rapidly and so can shoot up through dense vegetation and reach the light more quickly than can a plant which has to develop a stem thick enough to support itself.

The climbing habit has the disadvantage that the climbers are likely to fall with the death and decay of the plants on which they

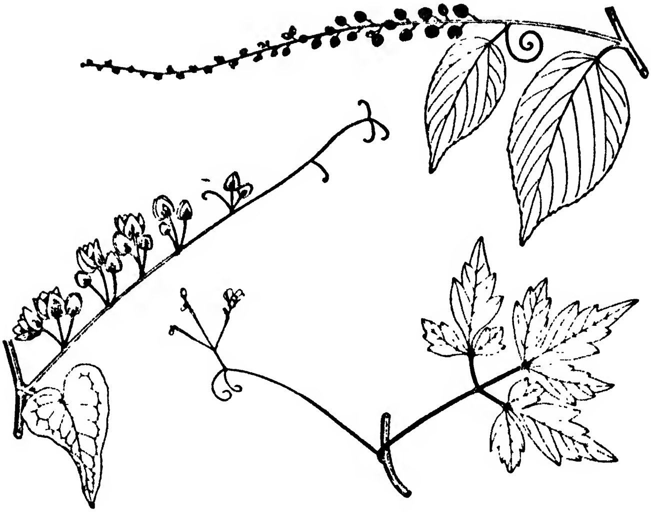


Fig. 197. Stems modified as tendrils

Above, *Guania microcarpa*; left, *Antigonon leptopus*; lower right, *Cardiospermum halicacabum*. (× ⅓)

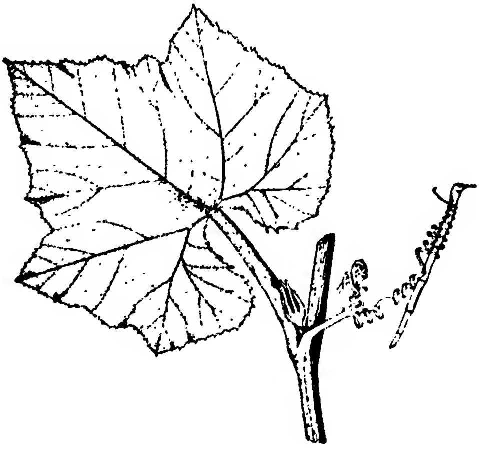


Fig. 198. Tendril of squash (*Cucurbita maxima*). (× ⅓)

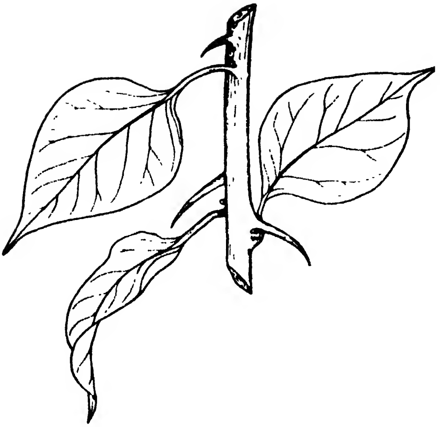


FIG. 199. Branches of *Bougainvillea* modified as spines used in climbing. (× ⅗)

grow. Frequently they grow over and shade the supporting plant to such an extent as to kill it, and thus are instrumental in bringing themselves to the ground.

In order to utilize the strength of some other object a plant must have some means of attaching itself to its support. There are four general types of climbers: *twiners, tendril climbers, root climbers*, and *scramblers*.

Twiners. A twiner climbs by the simple device of twining spirally around a support. In nature such a support would be another plant; in cultivation it is usually a wire, cord, or slender pole. The morning-glory is a common example of the twiners.

Tendril climbers. A tendril climber is held up by tendrils, which are either modified stems (Fig. 197) or leaves (Fig. 94) or are of doubtful homology, as in the squash family (Fig. 198). Tendrils are long, slender structures which coil around other objects or, more rarely, bear disks that adhere to the surface of the support.

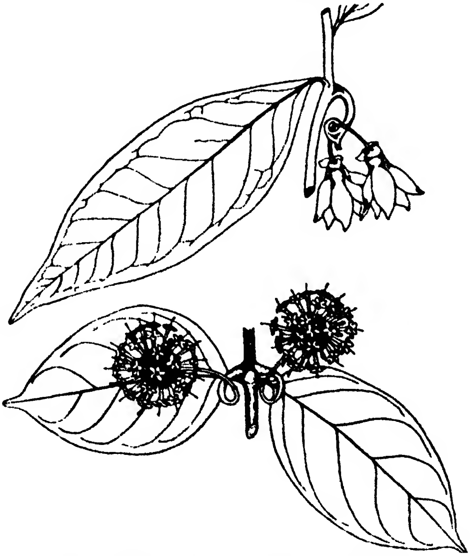


FIG. 200. Stems modified as hooks

Above, *Artabotrys uncinatus*; below, *Uncaria gambier*. (× ⅓)

Root climbers. Many climbers adhere to a support by means of numerous small roots which develop from the stem (Fig. 217).

Scramblers. Climbers of the scrambler type are not so definitely fastened to their support as are those of the other types. They are held up more loosely by means of thorns (Fig. 199) or hooks (Fig. 200). Climbing roses and raspberries are examples of thorn scramblers. Hooks are more advantageous than thorns, as they have a greater tendency to keep a plant from slipping backward. The thorns or hooks may be stem (Figs. 199, 200) or leaf structures. Rattans are excellent examples of scramblers with hooks on the leaves (Fig. 95).

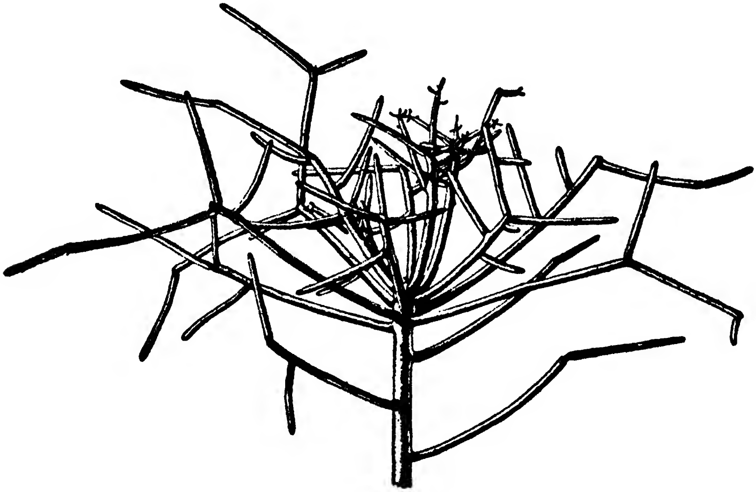


Fig. 201. Stems of *Euphorbia tirucalli* specialized for photosynthesis and water storage. (× ⅓)

Photosynthesis (leaf function). The young stems of green plants contain chlorophyll and carry on photosynthesis to some extent, and herbaceous stems continue to perform this function as long as they live. All green stems, therefore, perform to some extent the function which is the primary one of the leaf. In addition, numerous stems are specialized for photosynthesis and take the place of leaves in the manufacture of sugar. This is the case with the so-called asparagus fern and numerous sedges. Some stems which are specialized for photosynthesis are round (Figs. 81, 201, 202), others are flattened (Fig. 203), and others even have the form of leaves (Figs. 204, 205). Such stems as those of the cacti (Figs. 277, 279) are specialized both for photosynthesis and for water storage.

Absorption (root function). The epidermal walls of submerged water plants are not cutinized; consequently both the leaves and the stems of such plants are capable of absorbing water and substances in solution in water.

The stems of some parasitic plants produce emergences which enter the tissues of the host and absorb water and food material (Figs. 60, 61).

The function of anchorage, which is one of the chief functions of roots, is performed to some extent by underground stems (Fig. 206), as in cannas and many grasses.

Reproduction (seed function). Many plants reproduce by means of stems (Fig. 5), this being by far the most usual mode of vegetative reproduction in flowering plants.

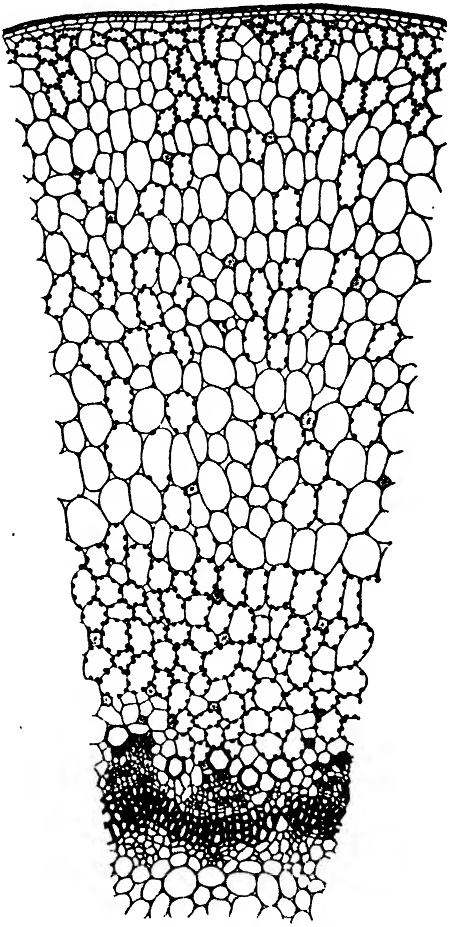


Fig. 202. Cross section of a portion of round stem of *Euphorbia tirucalli* (see Fig. 201) Note the wide cortex specialized for water storage and photosynthesis

Two of the most common methods of stem reproduction are by *rhizomes* (stems that grow horizontally in the soil) and by *runners*

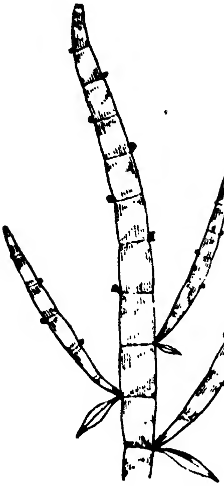


Fig. 203. Flattened stem of *Muehlenbeckia platyclada* specialized for photosynthesis. (× ½)

(stems that grow along the surface of the soil). Both rhizomes and runners may produce roots at the nodes. In some species the internodes do not persist long, and each new node forms a new plant. In other species an increase in the number of plants comes about only by the branching of rhizomes and the ultimate decay of the whole of the older portion formed before branching took place (Fig. 206). The method of reproduction by runners, and especially by rhizomes, is well suited to increasing the number of plants in a limited area or to the invasion of an area next to that in which the parent plants are growing. A new plant growing from a rhizome has a much better start than

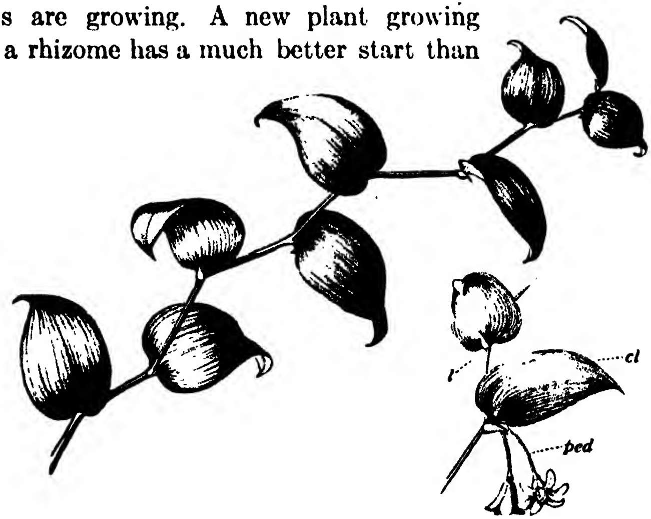


Fig. 204. Stem of *Myrsiphyllum*

l, scalelike leaf; *cl*, cladophyll, or leaflike branch, growing in the axil of the leaf; *ped*, flower stalk, growing in the axil of a leaf

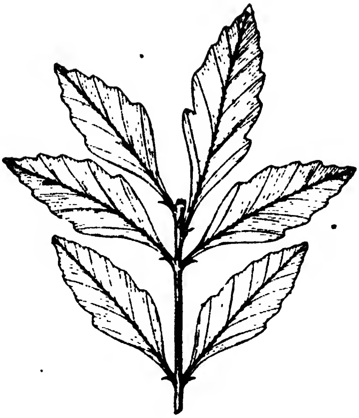


FIG. 205. Leaflike branches of *Phyllocladus protractus*. (× $\frac{2}{5}$)

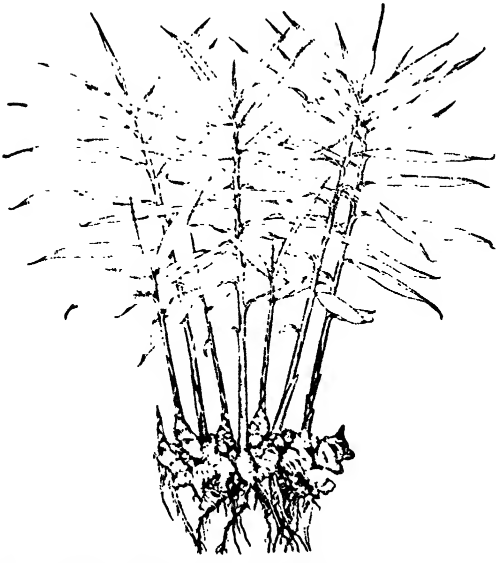


FIG. 206. Ginger plant with enlarged storage rhizome. (× $\frac{1}{7}$)

one growing from a seed, and, moreover, the rhizome is already in the ground, whereas the seed may never reach the soil.

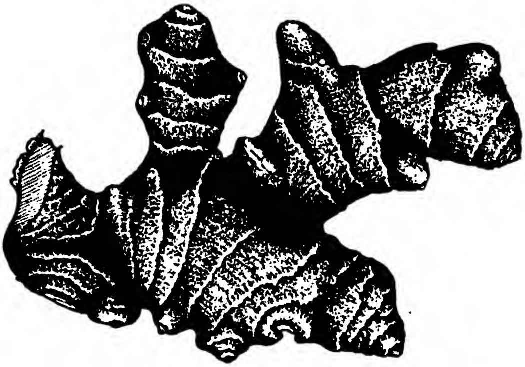


Fig. 207. Storage rhizome of ginger. (× ⅔)

Some stems grow up in the air at first and then, after they become long, bend down until they reach the ground, where they take root and so produce new plants.

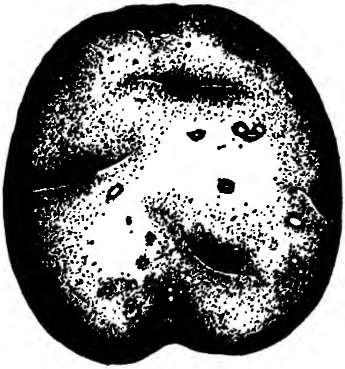


Fig. 208. Tuber of potato. (× ⅔)

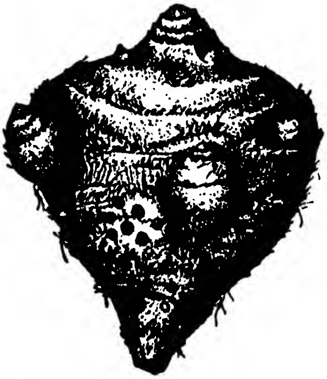


Fig. 209. Corm of taro (*Colocasia esculenta*). (× ⅔)

Storage. Except when the roots or leaves are fleshy and especially modified for food storage the stem is usually the chief organ in which food is stored. In large plants, food is stored at certain seasons in considerable quantities in the pith rays and the wood parenchyma.

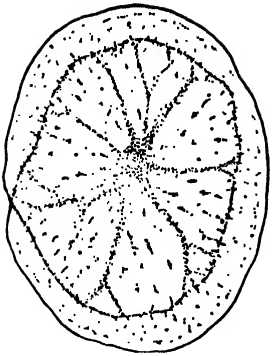


Fig. 210. Section of a potato tuber

The ring showing in the tuber is the cambium. Note that it comes near the surface at the bud, "eye."

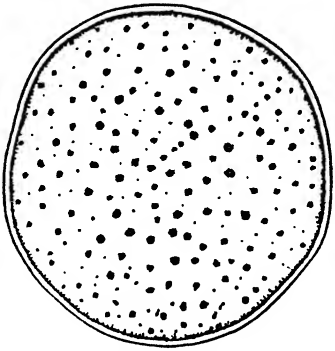


Fig. 211. Cross section of large stem of kohl-rabi

Note the thin cortex and the numerous vascular bundles with secondary thickening

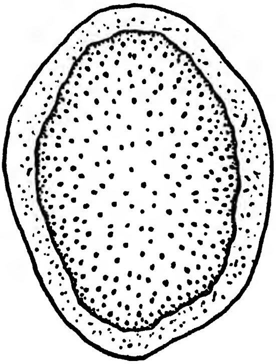


Fig. 212. Cross section of storage rhizome of ginger, a monocotyledon

Note that the cortex is clearly distinguished from the central cylinder. The scattered vascular bundles are evident. Compare Fig. 206

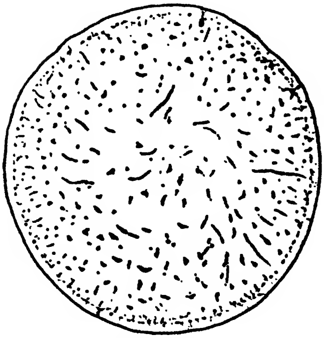


Fig. 213. Cross section of corm of taro (*Colocasia esculenta*)

Note the scattered arrangement of vascular bundles, characteristic of a monocotyledon

Some stems are especially modified for the storage of food. These are usually underground stems such as the *rhizomes* of ginger (Figs. 206, 207), the *tubers* of potatoes (Fig. 208), or the *corms* of aroids (Fig. 209). While most stems that are specialized for food storage are underground ones, there are exceptions. Some palms have greatly thickened stems in which large quantities of starch are stored during a series of years. This food is finally used up in the formation of flowers and fruits, after which the stem dies. Commercial sago is made from the starch stored in the trunk of the sago palm.

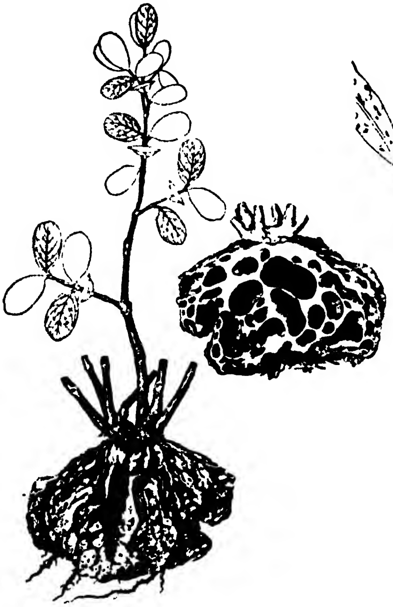


Fig. 214. *Hydnophytum*, an epiphytic plant

The swollen base of the stem is composed largely of water-storing tissue and contains cavities inhabited by ants. (× ⅓)

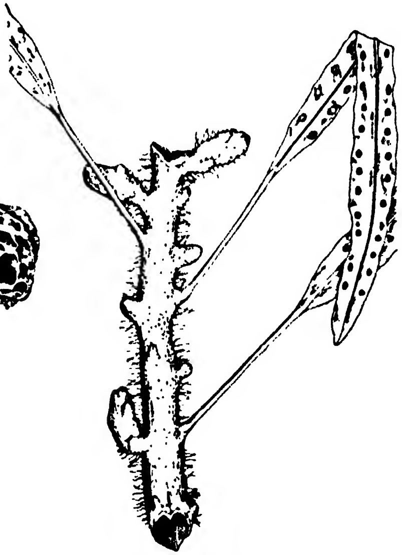


Fig. 215. *Polypodium sinatum*, a fern having hollow fleshy stems inhabited by ants. (× ⅓)

In the potato tuber, food is stored in both the central cylinder and the cortex (Fig. 210). Both regions are so modified as storage tissues that it is only by careful examination that they can be distinguished.

In kohl-rabi, which like the potato is a dicotyledon, the larger part of the thickened stem is composed of the central cylinder through which run numerous vascular bundles that show secondary thickening. The cortex is a thin outer layer (Fig. 211).

In ginger, a monocotyledon, the central cylinder and the cortex are clearly distinguished, though both are thickened (Fig. 212).

In the taro (*Colocasia esculenta*), another monocotyledon, food is stored largely in the central cylinder, and the cortex is relatively narrow (Fig. 213).

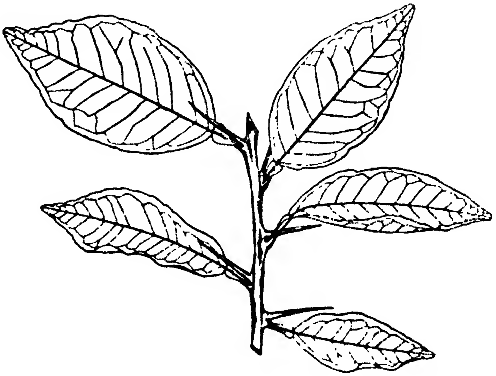


FIG. 216. Branches of lime (*Citrus aurantifolia*) modified as spines. (× ½)

There are stems which are especially thickened and modified for the storage of water. This is particularly true of the cacti (Figs. 277, 279).

In the Malayan region there are certain curious epiphytic plants that may be mentioned in this connection. The basal portion of the stem is greatly enlarged and consists mostly of water-storing tissue (Figs. 214, 215). In this basal portion are conspicuous labyrinthine cavities which are connected with the external atmosphere by means of small openings. The cavities are inhabited by ants. Various functions have been assigned to these cavities by different botanists, while others think that they have no particular function. Some regard them as devices for aeration, others consider that the ants which inhabit them benefit the plant by leaving debris from which the plant absorbs nutrient material, while still other observers believe that the ants serve as a means of defense for the plant.

Protection. The spines of many plants are modified branches (Figs. 199, 216). In some cases these spines protect the plants to some extent from being eaten by browsing animals.

CHAPTER XI

THE ROOT

In general the roots of a plant serve to absorb water and mineral matter from the soil and to anchor the plant in the ground. These may be said to be the chief functions of roots.

Absorption of water. The stems, leaves, and fruits of plants are usually exposed to high rates of evaporation in the air, from which they are protected by a covering that is more or less impervious to water. This coating not only reduces the amount of water that they lose through transpiration, but at the same time prevents them from absorbing water from the atmosphere. Such plants are therefore dependent on their roots for the absorption of water.

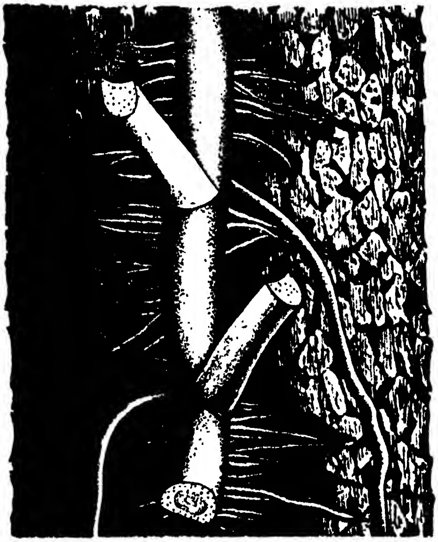


FIG. 217. Climbing stem of *Raphidophora*, showing short roots that attach the stem to the support, and long ones that grow to the ground and absorb water. (× ½)

Absorption of minerals. Plants need not only water, carbon dioxide, and oxygen, but also nitrogen, sulfur, phosphorus, potassium, calcium, magnesium, and iron. These last elements are obtained from the soil in the form of compounds dissolved in water. Some plants probably require, in addition, sodium and chlorine.

Anchorage. Plants that are growing in the ground need roots not only for the absorption of water and mineral matter but also in order that they may be anchored to the substratum; otherwise, erect plants would be blown over by the wind, while small creeping plants might be carried to unfavorable situations. There are three different types of root systems. Many dicotyledonous plants develop a long main root which grows deep in the soil and produces smaller secondary roots; such long roots are called *tap-roots*. In other cases the plant, instead of having a tap-root, is anchored in the ground by several large secondary roots. Monocotyledonous roots, like monocotyledonous stems, do not have secondary thickening, and so such roots never become very large. Monocotyledonous plants are usually anchored in the ground by numerous small roots. This is conspicuously the case with large palms such as the coconut.

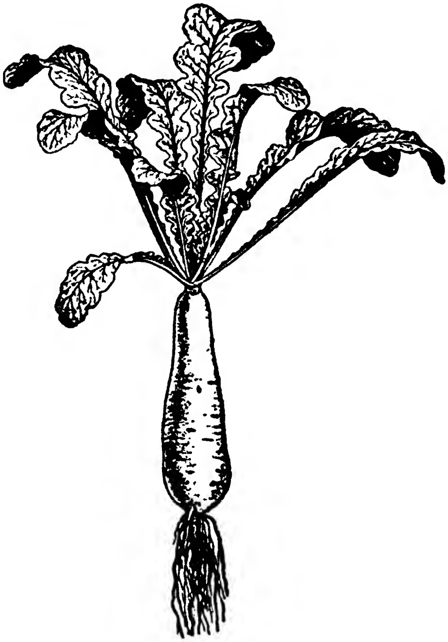


FIG. 218. Radish with greatly thickened storage root. (× ¼)

Aerial roots. Roots are characteristically subterranean structures, but they may develop in the air. Such is the case with many climbing plants (Fig. 217) and also with epiphytes (Fig. 2). In both of these cases the roots still have the functions of absorbing water and anchoring the plant. In epiphytic plants many of the roots grow so close to the bark of the plant on which they are found as to become attached to it; they are, at the same time, in a fairly favorable position for the absorption of water. Certain climbing plants develop two types of roots: small, short roots which anchor the plant to its support, and longer ones which reach down to the ground and serve more particularly for the absorption of water (Fig. 217).

Incidental functions. Roots have not only the two principal functions mentioned above but also functions that are incidental to these, as well as other functions, such as respiration, which are common to all plant parts. We shall find later that water absorbed by the roots is taken in very largely by the small young roots. In order that this water may reach the stem it must pass through the larger roots. In the same way manufactured food which comes down the stem from the leaves can reach the smaller roots only by passing through the larger ones. Thus it will be seen that roots, like stems, have the incidental function of conducting food and water. The cells in which such conduction is carried on are alike in roots and stems. Roots also, like stems, serve for the storage of food (the more safely for being underground) and are sometimes greatly thickened with storage tissue (Fig. 218).

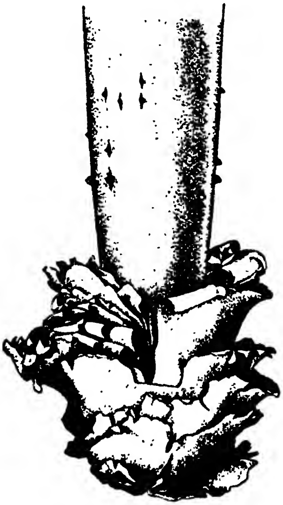


FIG. 219. Tip of aerial root of *Pandanus tectorius*, showing rootcap

See Fig. 234. (× ½)

GROWTH OF ROOTS

Rootcap. Roots are like stems in having at the tip a growing region, called the *growing point.* As the growing point is composed of meristematic cells which are soft and have thin walls, obviously it must be protected in some way; otherwise the meristematic cells would be destroyed while being pushed through the soil. This protective function is performed by a cap-shaped structure, the rootcap, which covers the growing point (Figs. 219, 221). The rootcap and the tip of the root are joined at the growing point, which consists of a small group of meristematic cells (Fig. 220). The outer part of the growing point produces cells that are added to the rootcap, while the inner portion forms cells which increase the length of the root.

The rootcap not only protects the growing point of the root but also serves as a boring point. It is especially fitted for this function because it is conical in shape, and probably even more so on account of the fact that the cell walls, or at least the middle lamellae of the old cells, become gelatinous. This makes the surface of the rootcap rather slimy, so that friction with the soil particles is greatly reduced and the tip can move through the soil more readily. As the rootcap is pushed forward through the soil particles the older cells are rubbed off and are replaced by younger ones which are produced from the meristem at the junction of the rootcap and the tip of the root.

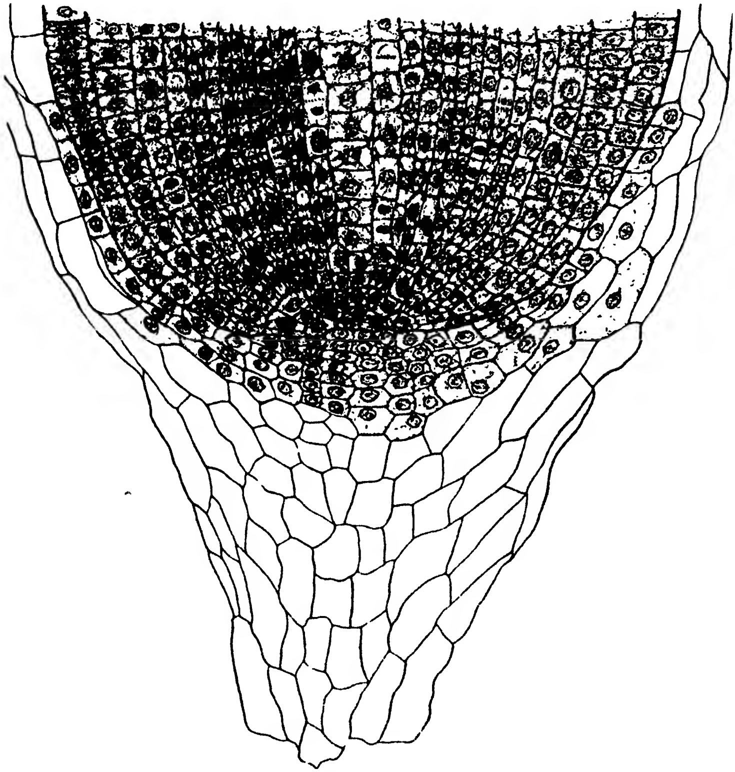


Fig. 220. Longitudinal section of a tip of an onion root

The growing point is in the center of the drawing and consists of three regions: one which produces the rootcap, one which gives rise to the cortex and epidermis, and one which forms the stele. (× 270)

Grand period of growth. A portion of a root, like any other part of a plant, has a grand period of growth which can be divided into a phase of formation, a phase of elongation, and a phase of maturation. As has been said before, the cells that add to the length of the root are produced on the basal side of the growing point. After these cells are cut off from the growing point they undergo a limited number of divisions. The part of the root in which division is most active is in the phase of formation, and the region in which this division occurs may be termed the region of formation. After dividing several times the cells derived from the growing point cease to divide, and elongate very considerably (Fig. 221). The region in which this is going on most actively is called the region of elongation, and the portion that is elongating is in the phase of elongation. The greatest increase in length of any portion of a root occurs while it is in this phase. Fig. 13 gives an idea of the elongation of one cell. After a portion of a root has reached its mature length the cells in that part take on their final characteristics. A region in which this is occurring is in the phase of maturation.

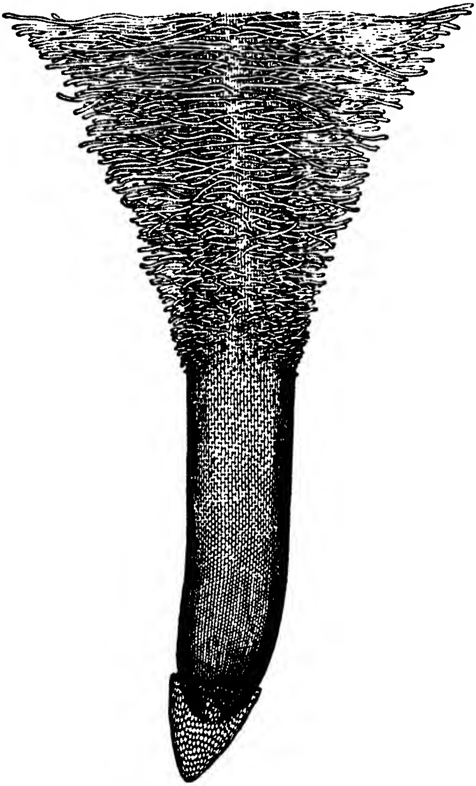


FIG. 221. Tip of root of millet

Below is the rootcap. Above the cap is the region of elongation, and above this a portion of the root-hair zone showing growth of root hairs. (× 35)

In the case of the root, as in that of the stem, the portion that is in the phase of formation grows slowly; at the end of the phase of formation the rate of growth increases, and continues to increase until the most rapid rate is reached during the phase of elongation; after this the rate of growth in length again decreases until, at the end of the period of maturation, growth ceases altogether. Growth is therefore most rapid not at the tip but slightly back of the tip in the region of elongation.

In general the region of elongation is much longer in stems than in roots. This is probably connected, in part at least, with the fact that the air offers very little resistance to the growth of stems, while the roots, in growing through the soil, meet with considerable resistance. If the elongating region of a root, which is composed of soft tissue, were of considerable length, the resistance offered to its movement through the soil would cause it to crumple.

ABSORPTION OF MATERIALS

Root hairs. We have seen that one of the principal functions of ordinary roots is to absorb water. It is therefore essential that they should have a large surface for the performance of this function, as the larger the absorbing surface the greater the rate of absorption. Enlargement of the surface is produced by the growth of long, slender projections from the cells of the outermost layer, or epidermis, of the root. These projections are called root hairs (Fig. 221). Root hairs are not cut off from the epidermal cells but are simply projections from them (Fig. 222). Most of the water absorbed by the roots is taken in by these hairs. They contain a lining of protoplasm within which is a large vacuole. As a root hair is the most active part of an epidermal cell, the nucleus is usually found in the root hair.

Since root hairs serve largely for the absorption of water, it is not surprising to find that many of the plants that grow submerged in water do not possess them.

Physical characteristics of the soil. In order to understand how roots absorb substances from the soil it will be necessary to consider the physical characteristics of the soil itself. The soil is made up of small irregularly shaped particles of rock and decomposing organic matter, with spaces between the particles. If the soil is well drained these spaces are largely filled with air. The water occurs as very thin films which adhere to the soil particles. The force by which this water is held is very great; it is so great that the water cannot all be removed by evaporation without the application of heat.

The air found between the soil particles is essential to the respiration of the roots of most plants. The presence of air can be very clearly demonstrated by putting a mass of soil under water, when the water will displace the air in the spaces and the air will be seen leaving the top of the soil in the form of bubbles. Many plants cannot live in a soil that is flooded, as such a soil does not contain sufficient oxygen for the respiration of their roots.

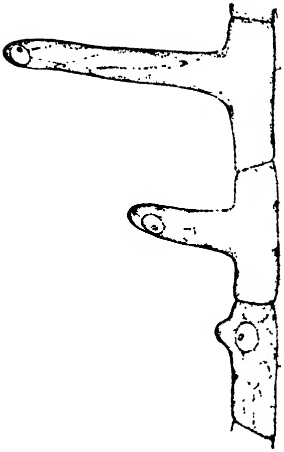


Fig. 222. Section showing the formation of root hairs in millet root. (× 280)

Contact of root hairs with soil particles. The formation of root hairs aids in the absorption of water not only because it increases the absorbing surface but also because the hairs come in closer contact with the soil particles than would be possible in the case of large roots.

Growth of root hairs. Root hairs tend to grow out at right angles from the surface of the roots, but when they are in the soil they soon meet with soil particles and are thus turned aside. In doing this their surfaces conform to those of the particles around which they grow, so that they are in very intimate contact with the soil particles. Growth in root hairs occurs only at the tip, which is protected by having a thickened wall (Fig. 222). Growth at any point other than the tip would loosen the attachment of the hairs to the soil particles.

Location of root hairs. Root hairs do not occur at the tip of the root or in the region of elongation. If they did occur in these places, they would, on account of their close contact with the soil particles, be likely to be broken as the tip was pushed through the soil. Root hairs are ephemeral structures, and after they have functioned for a short time they dry up and disappear, so that they occur in only a short zone, which is called the *root-hair zone.*

Anchorage by root hairs. The close contact of the root hairs with the soil particles is of advantage in more ways than simply for absorbing water and minerals from the soil. The contact with the soil particles is so close that when the root is pulled from the soil either the hairs are broken off or the soil particles adhere to the roots (Figs. 223, 224). This adhesion of the hairs to the soil particles aids in anchoring the plant in the ground. It is also of advantage in that the part of the root which bears the root hairs is firmly anchored, so that when the more apical portion increases in length the root-hair zone is held firmly in position and the tip is shoved forward.

Absorption of water. The cell wall of the root hair is lined with a thin layer of protoplasm, within which is a large vacuole that has sugar and other substances dissolved in it. The protoplasm acts as a semipermeable membrane around the vacuole, while the plasma membrane which bounds the cytoplasm is a semipermeable membrane around the remainder of the protoplasm. The osmotic pressure in the root hair is greater than that of the surrounding soil water, and so water is drawn from the soil into the root hair. Osmotic pressure is also instrumental in causing the movement of water from cell to cell in the cortex of the root.

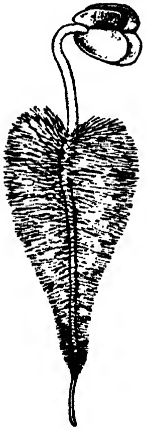


FIG. 223. Seedling of radish, showing root hairs grown in moist air. (× 1½)

Passage of water through the cortex. When water passes into a root hair, it goes from a solution with a low osmotic pressure to one with a high osmotic pressure; when it passes from the parenchyma cells to the vessels, the reverse is the case; but the water is frequently forced into the vessels under considerable pressure. This is clearly shown in the bleeding, or exudation of water, from the stems of many plants after the upper part of the plant has been removed. The bleeding seems to be due to great turgidity and high turgor pressure in the parenchyma cells. When pressure within the cells becomes sufficiently great, water and other substances to which the protoplasm is permeable appear to be forced out of the cells under pressure; but this process is not fully understood.

Turgor pressure. The pressure of bleeding is often designated as root pressure because when plants are turgid the roots usually produce such a pressure. *Turgor pressure* is a more appropriate name, however, as pressure of a similar nature may be produced in other parts of plants.

Turgor pressure of roots cannot be considered as an explanation of the movement of water up the stem, as such pressure can occur only when the parenchyma cells of the root are turgid, and this is not usually the case when transpiration is active and the movement of water most rapid. At such times there is little or no turgor pressure, and water may be absorbed by the stump of a decapitated stem instead of being exuded from it.

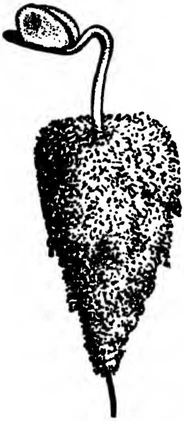


Fig. 224. Seedling of radish from seed planted in the soil

Note the adherence of soil to root hairs and compare with Fig. 223. (× 1½)

Bleeding is largely responsible for the exudation of maple sap or the sweet juices from palm inflorescences (Figs. 155, 156) that have been cut and that yield sugar or, after fermentation, produce alcoholic beverages or vinegar. The Mexican alcoholic beverage known as pulque has a similar origin, as it is the fermented juice obtained from agave plants from which the buds have been removed.

Absorption of minerals. The water around the soil particles contains mineral matter which is dissolved from the soil. This water is in contact with that in the cell wall of the root hair, and so is continuous with it, while the water in the cell wall is in turn continuous with that in the interior of the hair. The mineral matter dissolved in the soil water tends to diffuse into the water in the cell wall, and through that into the interior of the cell. In this way mineral matter passes from the soil into the plant. While in the root hairs the plasma membrane, or outer layer of protoplasm, is impermeable to sugar and many other substances within the cell, it is permeable to many of the simple inorganic compounds found in the soil. The diffusion of the mineral matter through the plasma membrane is independent of the movement of the water.

By the use of a piece of parchment paper separating a solution of sugar from pure water it is very easy to demonstrate that the movement of a solvent and the movement of the solute through a membrane may be independent of each other. The volume of the sugar solution will increase, showing that it has absorbed water, while at the same time some of the sugar will pass in the opposite direction into the pure water. The movement of water in one direction and of a dissolved substance in the opposite direction through the same membrane at the same time can be strikingly shown by the use of the thistle-tube apparatus shown in Fig. 75. The bulb of the thistle tube is filled with concentrated sugar solution, a piece of parchment paper is tied over the mouth of the bulb, the tube is inverted, and the bulb is immersed in distilled water. Water is drawn into the sugar solution, as is shown by the fact that the latter rises in the thistle tube. If now we repeat the same experiment with the addition of coloring the sugar solution with eosin, the sugar solution still rises in the tube while some of the eosin passes out through the parchment paper and colors the distilled water. In other words, the movements of the eosin and the water are independent.

Accumulation of mineral matter in a plant. As movement by diffusion is always from a greater to a less concentration, a given kind of mineral matter would be expected to enter a plant only so long as the concentration of that particular substance was greater outside than inside the plant. The original substance, however, after entering a plant, is usually combined with others in such a way that it no longer exists in the same form as in the soil water. In this way the concentration of a given substance may remain greater outside than inside, even though it is absorbed in large quantities. Owing to this fact a plant may accumulate a much greater proportion of a given element than is found in the soil water.

Inasmuch as the diffusion of mineral matter dissolved in water is independent of the diffusion of the water itself, an increase in the amount of water absorbed by a plant would not increase the amount of mineral matter absorbed if the water moved in the plant only by diffusion. It is only owing to the fact that the water in the vessels moves as a steady stream, and not by diffusion, that transpiration can increase the amount of mineral matter taken in by a plant.

It is indeed questionable how far transpiration can cause an accumulation of mineral matter in a plant. If any given mineral substance should accumulate anywhere in the plant in greater concentration than it occurs in the soil, it would tend to diffuse to a region of lower concentration and finally to the soil water. It is only as a given mineral substance is changed into some other substance that the elements composing it can accumulate in the plant to a much greater extent than that in which they occur in the soil water.

Elements obtained from the soil. There are ten elements which are universally regarded as essential for the higher plants. The three which are found in carbohydrates (that is, carbon, hydrogen, and oxygen) are obtained from carbon dioxide and water. Carbon comes from carbon dioxide, hydrogen from water, and oxygen from both carbon dioxide and water.

There are seven elements which must be obtained from the soil. These are nitrogen, sulfur, phosphorus, magnesium, iron, calcium, and potassium. Three of these are necessary for the manufacture of plant proteins. These are nitrogen, sulfur, and phosphorus. Nitrogen is a prominent constituent of all proteins; sulfur is found in proteins in small amounts, but nevertheless is necessary for the building up of plant proteins; phosphorus is an essential constituent of the conjugated proteins of the nucleus.

Two of the mineral elements from the soil are necessary for the formation of chlorophyll. These are iron and magnesium. Iron does not enter into the chlorophyll molecule, but chlorophyll cannot be formed except in the presence of iron. Magnesium is one of the elements in chlorophyll.

Calcium is a constituent of the calcium pectate of the middle lamella. Calcium is often deposited very abundantly in the form of calcium oxalate, which is a combination of calcium and oxalic acid (Figs. 22–24). The calcium appears to neutralize the harmful effect of the oxalic acid which is formed as a by-product of metabolism. Potassium is needed in considerable quantities, and appears to play an important role in vital activities, as it is abundant in meristematic regions and cells rich in protoplasm.

The above account is by no means a complete description of the physiological uses of the elements mentioned. The functions of some of the mineral elements are very complicated and are often rather obscure.

SOIL

Texture of soil. Soils are composed of particles which are classified according to their size as *gravel*, *sand*, *silt*, and *clay*. These divisions are arbitrary, and the size limits assigned to the various classes by different authorities are not always the same. Particles over 1 millimeter in diameter may be regarded as gravel or rock; those between 0.05 millimeter and 1 millimeter, as sand; those between 0.005 millimeter and 0.05 millimeter, as silt; and those less than 0.005 millimeter, as clay. A soil containing a large proportion of sand is called a sandy soil, one with much clay a clay soil, while soils that are intermediate are *loams*.

The amount of water held by a soil varies with the total surface of the particles, and so clay, being more finely divided than sand, holds more water than sand, which dries out rather quickly.

Movement of water in soil. During a rain, water enters the spaces in the soil and expels the air. The action of gravity tends to carry the water down into the soil, but films are left around the soil particles. The downward movement of the water is known as *percolation*. After the rain has ceased, air is drawn into the soil as the water moves downward. Percolation continues until it reaches a region (the *water table*) in which all the spaces are occupied by water. The percolation of water is most rapid in coarse soils and slowest in fine soils. In clay soil, percolation may be so slow that after the upper layers have become saturated much water runs off the surface, while the underlying layers remain relatively dry.

The percolation of water is very important, as by this means a reserve supply is carried to lower levels. The soil loses water by evaporation from the surface, with the result that water is drawn up from the lower levels in much the same way as oil moves up a wick. Also, when a plant absorbs water from the soil particles in contact with the root hairs, water is drawn from more moist particles to those from which the plant has taken water. It is owing to this movement of soil water that a soil dries out rather uniformly.

Water is drawn up in loam more rapidly than in sand or clay. The attraction of a soil for water increases with the total surface of the particles; consequently loam draws water with greater force than does sand. According to this reasoning we should expect clay to draw water more rapidly than loam; but clay is composed of such small particles, and the spaces between the particles are so small, that water is held with great force and there is less tendency for the water to percolate or be drawn up than in the case of loam.

Loam allows sufficient water to percolate through it, and then draws it up again with considerable rapidity. For this reason loam is better for agricultural purposes than is either sandy soil or clay. Moreover, the air spaces are large enough to allow for sufficient aeration, which is not likely to be the case with clay.

The upward movement of water takes place in the films around the particles, and so any interference with the continuity of the films tends to retard the movement. Water can be conserved by working the soil near the surface into a mulch, or loose layer, as by this means the continuity of the films is interrupted, so that water is not drawn to the surface, where it would be lost by evaporation. That water is drawn to the surface to a greater extent in compact than in loose soil is shown in the case of footprints in a cultivated field. The soil under the footprints is more compact than the surrounding soil, and has a darker color due to the greater amount of water that it contains.

Soil structure. The term *soil structure* is used to denote the manner in which the particles are arranged in a soil. When the fine particles are aggregated in granules, the soil is said to have a granular, or crumb, structure. Such a soil is loose and friable and is considered to be in good physical condition. If a clay soil is worked when it is wet, the granular structure is destroyed and the soil becomes compact and poorly aerated. The soil is then in poor physical condition. The wet condition is very persistent, and at the same time the soil is impervious to the percolation of any water. As the clay soil in this wet condition dries it shrinks and cracks, thus forming hard, tenacious clods.

Weight of soil. A given volume of sand is heavier than the same volume of clay, as the weight of the individual grains of sand is sufficient to overcome considerable friction and to cause the particles to be compactly arranged, so that the pore space is decreased to a greater extent than is the case with lighter particles such as clay.

Water has a tendency to bind soil particles together, as is shown in the case of sand, which can be molded to some extent when wet but falls apart when dry. Owing to the greater amount of surface afforded by the small particles of clay, water binds particles of clay together with much more force than it does grains of sand. It is partly for this reason that clay is tenacious and harder to plow than sand, and it is owing to these properties that a farmer regards clay as a heavy soil and sand as a light soil.

Water absorption and transpiration. When soil contains a considerable quantity of water, it gives up water to plants more readily than when it is dry. The amount of water in the soil may therefore be a very important factor in determining whether or not a given rate of transpiration is excessive. In order that a plant may live it must, over an extensive period, absorb as much water as it loses through transpiration. If the rate of transpiration continues to be greater than the rate of absorption, the plant will ultimately wither and die. When there is a sufficient supply of water in the soil, a plant may be able to replace the amount of water lost, even when the rate of transpiration is comparatively high; if there is less water in the soil, the same rate of transpiration may cause the plant to succumb to drought.

Available soil moisture. Plants not only cannot absorb water as rapidly from a dry soil as from a moist soil, but they will wilt long before all the water is removed from the soil. When the water is reduced below a certain amount, a plant cannot absorb it fast enough to replace loss through transpiration, and so wilting ensues. Therefore not all the water that is in the soil is available. The percentage of water that is left in a soil when a plant wilts is called the *wilting coefficient* of that soil. This wilting coefficient varies with different soils, being higher with fine soil than with coarse soils. It also varies with the rate of evaporation, as a plant will wilt with more water in a soil when the rate of transpiration is high than when it is low.

Effects of cultivation. Cultivation destroys weeds and renders the soil more porous, so that it is better aerated, water is absorbed readily, and roots can penetrate it easily. As has already been pointed out, cultivation of the surface layers may decrease the amount of water lost from the soil through evaporation.

Humus. Soils contain varying quantities of dark-colored decaying organic matter known as humus. It is owing to the presence of humus in soil that the soil is usually darker-colored than the subsoil. As a source of nitrogen, humus is a very important constituent of soils. It is also valuable in other ways. Humus has great capacity for absorbing water and so may have great value in increasing the water-holding capacity of a soil. Clay soil is rendered more porous by the presence of humus.

Organisms in the soil. In addition to containing the roots of plants, the soil is the home of a large variety of organisms which have great influence on soil fertility. Green plants can utilize materials only when they are in the form of simple compounds, and so the remains from plants and animals must be decomposed before they are available to the higher plants. Animals take part in this process. Earthworms break down organic materials and also mix the soil. Bacteria and fungi are very numerous in the soil and are most important agents for the decomposition of organic material. When nitrogenous compounds are broken down, the chief end product is ammonia. In the soil are bacteria which oxidize the ammonia to nitrites and others which oxidize the nitrites to nitrates, the form in which nitrogen is most readily absorbed by green plants. These nitrifying bacteria are very important in preserving the fertility of the soil, because without them much of the ammonia, which is a gas, would escape and be lost in the atmosphere. From the standpoint of soil fertility other soil bacteria known as nitrogen-fixing bacteria are most important. These bacteria have the ability to assimilate the free nitrogen of the air; through their activity combined nitrogen is added to the soil and can be used by higher plants. Nitrifying and nitrogen-fixing bacteria are described at greater length in a later chapter.

THE ANATOMY OF ROOTS

General regions. The general internal structure of stems and roots is very similar. In both cases there is a central stele which is surrounded by a cortex (Figs. 225, 226). In stems this is in turn surrounded by an epidermis. Some authorities maintain that in roots there is no true epidermis, but that this structure is represented morphologically in the formation of the primary rootcap. Others, however, contend that the outermost layer of the root is morphologically an epidermis, but that it is not such physiologically, as it is an absorbing and not a protective structure. These theoretical considerations need not concern us here; for the sake of simplicity we may regard the outermost layer of the root as an epidermis.

Epidermis. The epidermis of a root is, as we have seen, very different in structure and function from that of stems and leaves, but agrees with that of the latter in being a single layer of cells.

Roots that grow underground are not exposed to high rates of evaporation, and so they do not need to have cutinized walls to protect them from transpiration. Moreover, if their walls were cutinized or thickened, this would interfere with the absorption of water. The walls are thin, soft cellulose membranes. The principal peculiarity of these cells consists in the presence of the long root hairs, the structure and function of which have already been discussed.

Stele. The general structure of monocotyledonous and dicotyledonous roots is very similar (Figs. 226, 227). This applies to the arrangement of vascular bundles as well as to other features, and is strikingly in contrast with the great difference in arrangement of bundles in monocotyledonous and dicotyledonous stems.

The stele of roots is usually much smaller in comparison with the cortex than is the case with stems (Figs. 226, 227). This is due to the greater centralization of the thick-walled elements in roots than in stems, which is connected with the fact, as previously explained, that the stress which roots have to withstand is largely longitudinal tension.

The center of the stele may be occupied by thin-wall pith cells, by thick-walled sclerenchymatous cells, or by one or more xylem

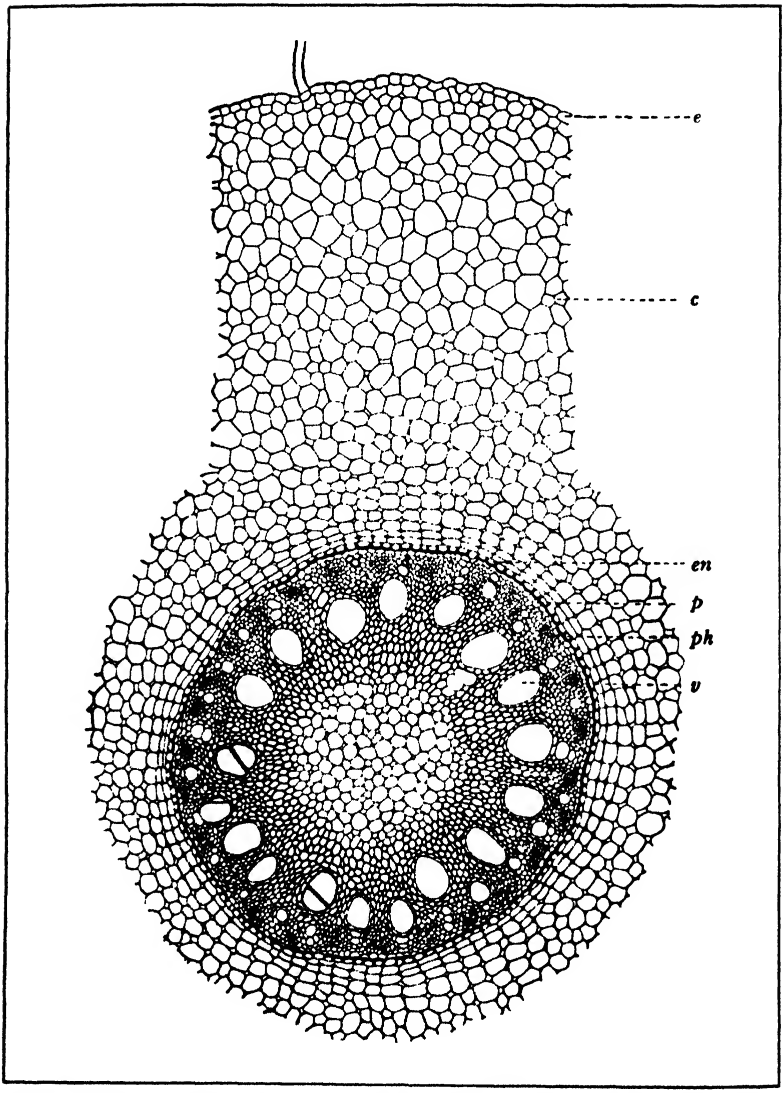


FIG. 225. Portion of section of root of a monocotyledonous plant (*Hedychium coronarium*), showing stele and portion of cortex and epidermis

e, epidermis; *c*, cortex; *en*, endodermis; *p*, pericycle; *ph*, phloem; *v*, xylem vessel. (× 85) vessels. Around this central portion the xylem, as seen in cross section, is arranged in rays which are usually widest near the center and taper toward the outside (Figs. 226, 227). The phloem occurs in groups between the xylem regions, and not exterior to the xylem, as in stems. The alternate arrangement of the xylem and phloem is apparently connected with the absorbing function of roots. As the phloem is not at the outside of the xylem, water may pass straight from the epidermis to the xylem without going through the phloem.

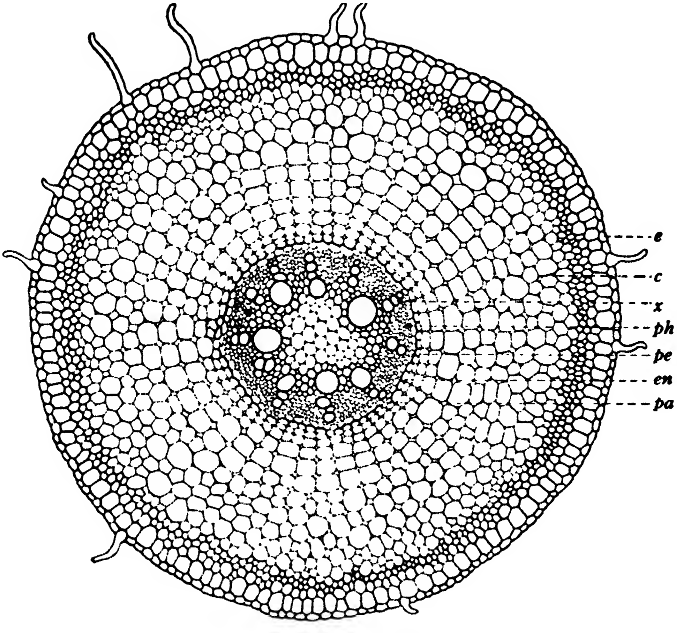


FIG. 226. Cross section of root of a species of Wandering Jew (*Commelina*), a monocotyledonous plant

e, epidermis; *c*, cortex; *en*, endodermis; *pa*, passage cell; *pe*, pericycle; *ph*, phloem; *x*, xylem. (× 55)

Pericycle. The outermost part of the stele is, as in stems, the pericycle. In roots the pericycle never contains sclerenchyma cells but is composed altogether of parenchyma cells, and usually consists of only a single layer (Figs. 226, 230).

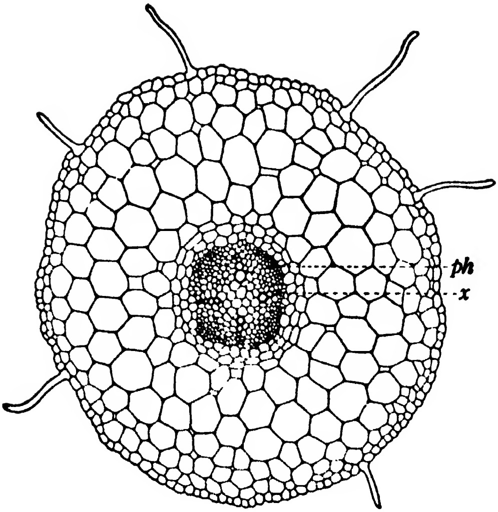


Fig. 227. Cross section of young root of a dicotyledonous plant, mungo bean (*Phaseolus radiatus*)

In the stele there are four rows of xylem vessels, the protoxylem, one of which is labeled *x*. Alternating with the xylem is the phloem, *ph*. (× 70)

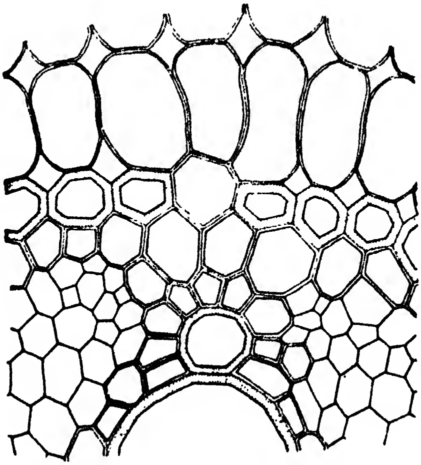


Fig. 228. Cross section of a portion of root of Wandering Jew (*Commelina*), showing endodermis and passage cell

The endodermis is a row of thick-walled cells running across the drawing; the passage cell is the thin-walled cell in this row. Note the xylem below the pas- cell. (× 300)

Cortex. The cortex lies between the stele and the epidermis. The innermost layer of the cortex in the stem is known as the starch sheath. In roots this layer is called the *endodermis.* The walls of the cells of the endodermis, and particularly the radial ones, are partially cutinized. The walls may remain thin (Fig. 230) or they may be thickened (Figs. 225, 226). In the latter case all the walls may be equally thickened, but usually the radial and inner walls are thicker than the outer walls. Certain cells found in the endodermis near the ends of the xylem rays (Figs. 226, 228) remain thin-walled as long as that part of the root is absorbing water through its root hairs. Such thin-walled cells are called *passage cells* and apparently serve as passageways for water going from the cortex into the stele. An endodermis containing thick-walled cells and passage cells appears to direct the movement of water so that it shall pass directly to the xylem and not through the phloem. Thus it enters the xylem and is conducted upward without getting into the sieve tubes and diluting their contents. In old parts of roots the cortex often disappears and the endodermis functions as an epidermis (Fig. 232).

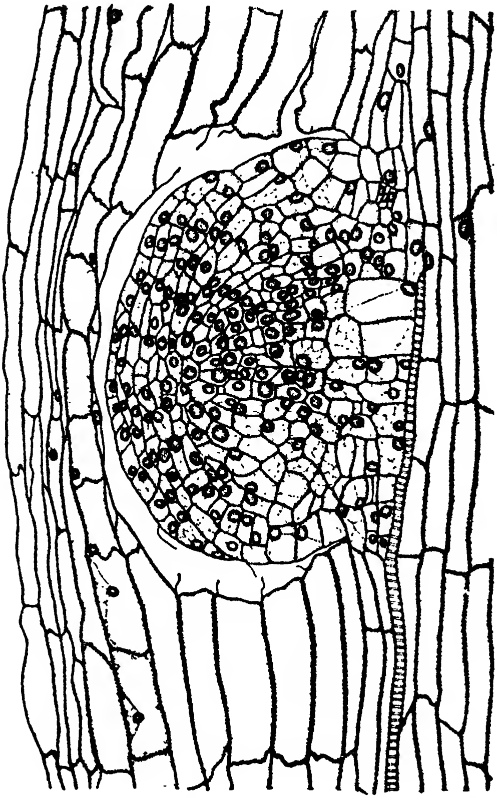


Fig. 229. Longitudinal section of a portion of an onion root, showing internal origin of branch root. (× 175)

The endodermal cells fit close together, so that there are no air spaces between them. As there are air spaces between the other cells of the cortex, the lack of them in the endodermis would appear to decrease the diffusion of air into the vascular tissues.

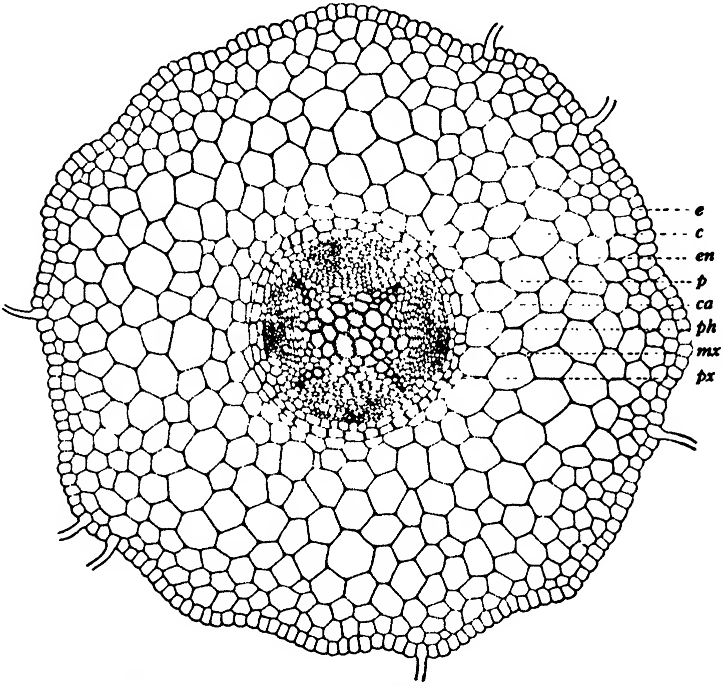


Fig. 230. Cross section of root of mungo bean (*Phaseolus radiatus*) older than that shown in Fig. 227

e, epidermis; *c*, cortex; *en*, endodermis: *p*, pericycle; *ca*, cambium region; *ph*, phloem; *px*, protoxylem; *mx*, metaxylem. (× 85)

The part of the cortex outside of the endodermis is frequently composed of parenchyma cells only. These cells may serve for the slow movement and storage of food. As in the case of stems, the cortex in young roots is of importance in giving rigidity. This is done by means of turgor. The epidermis of the root is usually an ephemeral structure. In many cases the cell walls of the outer layers of the cortex become thickened, and these layers take the place of the epidermis.

The cortex of the root does not contain collenchyma, as does that of many stems. In stems the collenchyma usually forms a continuous band in the outer part of the cortex. As was previously explained, this distribution of collenchyma is connected with the resistance which stems have to offer to bending stresses. As roots are not subject to the same type of stresses, there is not the same necessity for the development of collenchyma.

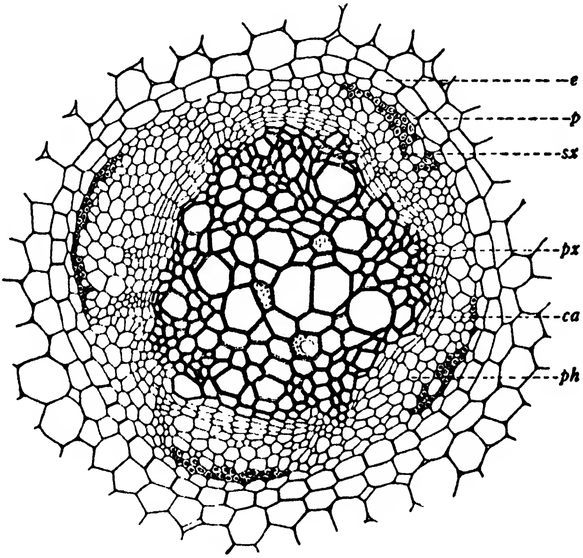


Fig. 231. Cross section of central portion of root of mungo bean (*Phaseolus radiatus*) after secondary xylem has been formed from the cambium

e, endodermis; *p*, pericycle; *ph*, phloem; *ca*, cambium; *px*, primary xylem; *sx*, secondary xylem. (× 115)

Roots that are in the ground cannot carry on photosynthesis, and in such cases chlorophyll is not developed in the cortex. In roots which normally are exposed to the light, however, chlorophyll is frequently developed in the parenchyma cells of the cortex, and in this case the cells are chlorenchyma cells.

Branch roots. The branches of stems originate as superficial outgrowths in which both the epidermis and the underlying tissues take part. The cortex and epidermis of the branch and those of the main stem are therefore continuous. In roots, on the other hand, a branch originates in the pericycle and forces its way through the cortex and epidermis, breaking these tissues as it grows (Fig. 229). Owing to their method of origin, therefore, the epidermis and the cortex of a branch root are not continuous with the epidermis and the cortex of the main root.

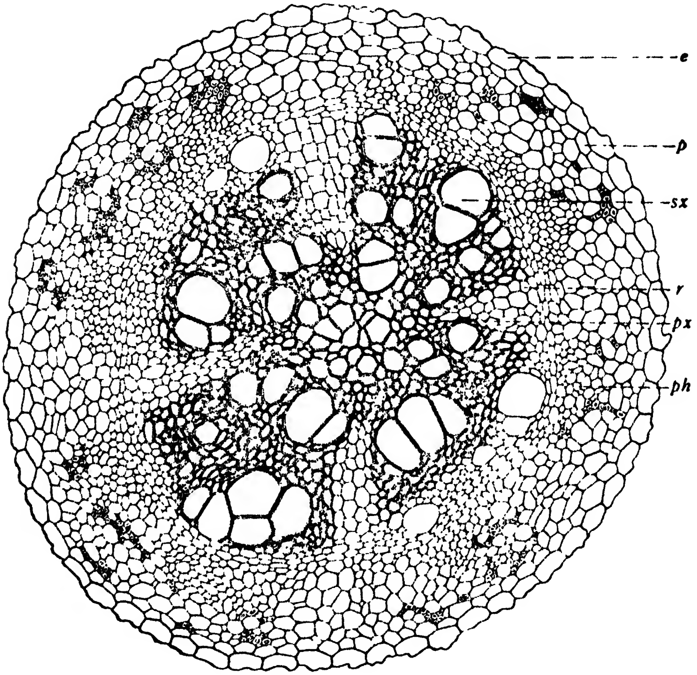


Fig. 232. Cross section of root of mungo bean (*Phaseolus radiatus*) after all of the cortex except the endodermis has disappeared

e, endodermis; *p*, pericycle; *ph*, phloem; *px*, primary xylem; *sx*, secondary xylem; *r*, pith ray. (× 80)

Secondary thickening. Dicotyledonous roots, like dicotyledonous stems, increase in thickness owing to the activity of the cambium. In very young roots there is no cambium (Fig. 227). The beginning of the process of secondary thickening is initiated by the formation of a cambium in the stele on the inner side of each of the groups of phloem (Fig. 230). Subsequently this cambium extends around the outer end of the rays of the xylem, so that it forms a convoluted cylinder (Fig. 230). By the activity of the cambium, secondary phloem is formed on the inner side of the primary phloem. The secondary xylem is not formed next to the primary xylem but opposite the secondary phloem (Fig. 231), while a pith ray is formed exterior to each of the primary rays of xylem (Figs. 231, 232). Although at first the cambium has the form of a convoluted cylinder, the convolutions are soon straightened out by unequal rates of growth in different places, and the cambium, as seen in the cross section, becomes a regular circle (Fig. 232). The subsequent activity of the cambium in the root is similar to that in the stem.

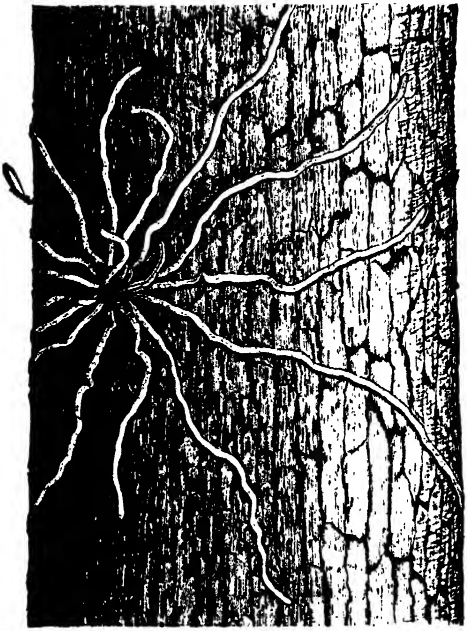


FIG. 233. *Taeniophyllum*, a leafless epiphytic orchid with roots which serve for photosynthesis. (× $\frac{2}{5}$)

SPECIALIZED ROOTS

The chief functions of roots are the absorption of water and mineral matter and the anchorage of the plant. Some parasites have specialized roots that produce haustoria (Fig. 8) which perform these functions. Moreover, roots, like other organs, may be specialized for functions which are not, in general, characteristic of the organ concerned.

Such specialized roots may be classified according to their functions under the following headings: *photosynthesis* (leaf function), *support* (stem function), *reproduction* (seed function), *storage*, and *aeration*.

Photosynthesis (leaf function). Underground roots are not exposed to the light, and so are not in a position to carry on photosynthesis. Such roots do not develop chlorophyll. The roots of many epiphytes and of some vines, however, are exposed to the

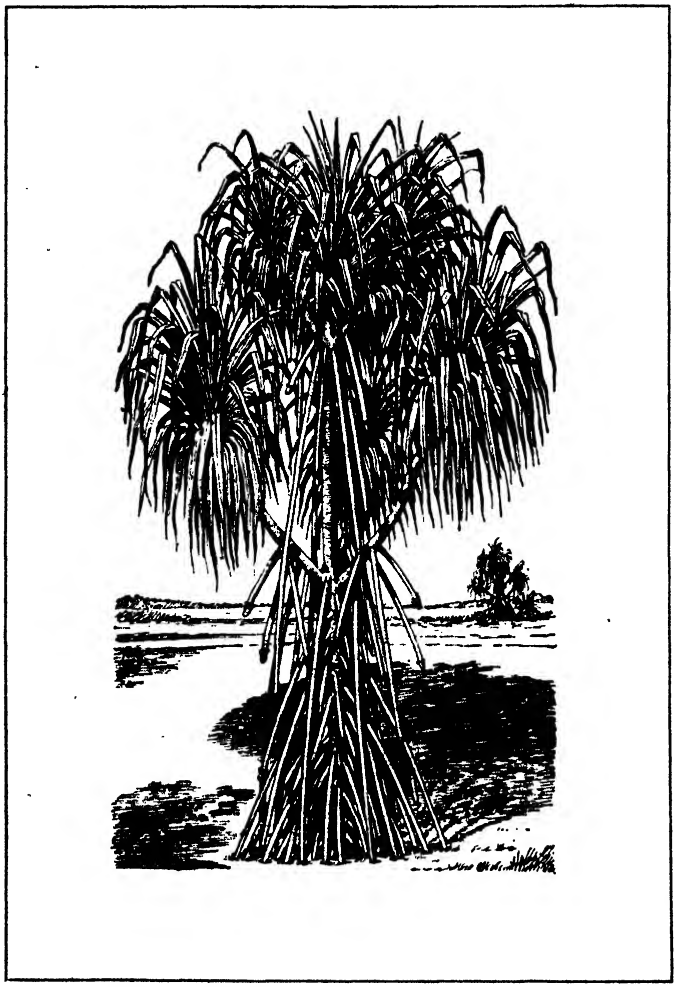


Fig. 234. *Pandanus tectorius* with prop roots. (× $\frac{1}{35}$)
This plant is very common along the strand in the Eastern tropics and is planted throughout the tropics as an ornamental plant

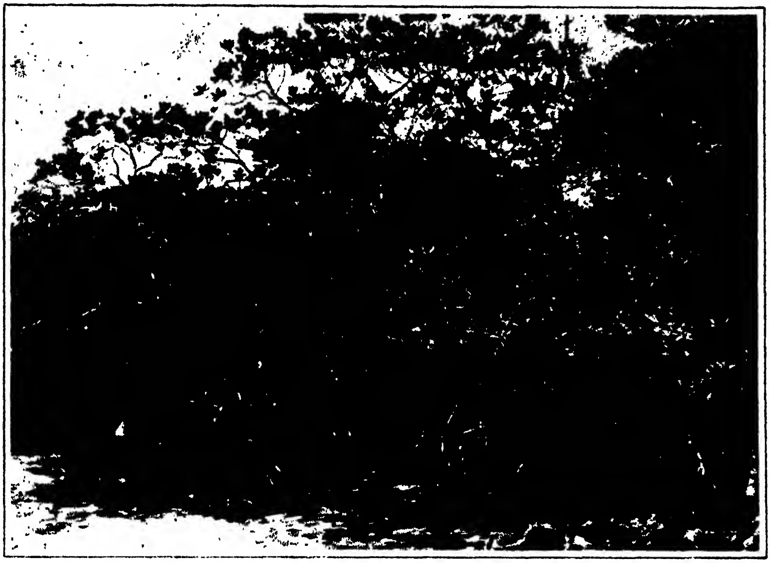


Fig. 235. Prop roots of *Rhizophora candelaria*

These roots have a great development of air spaces in which oxygen diffuses to the underground portions of the root system. *Rhizophora* is one of the principal plants in the mangrove swamps described in Chapter XII, Plant Geography

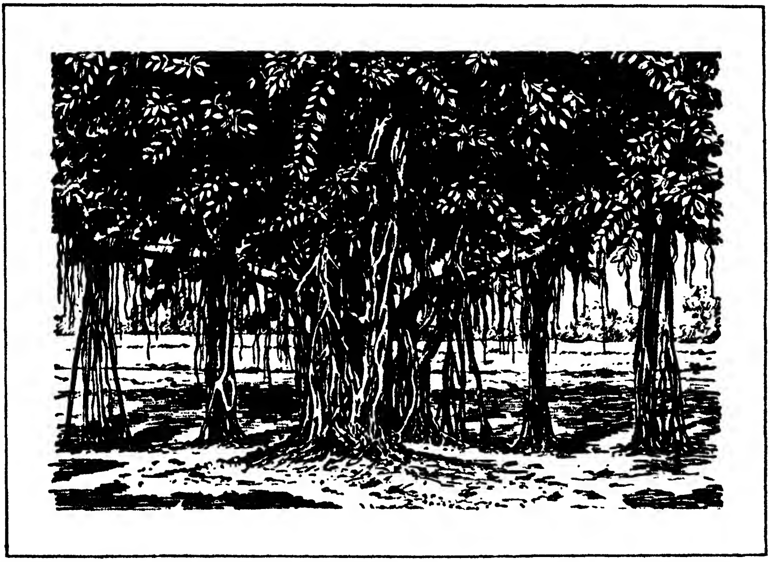


Fig. 236. India rubber tree (*Ficus elastica*) with roots forming secondary trunks

light, and such roots usually possess chlorophyll and so manufacture food by means of photosynthesis. In the epiphytic orchid *Taeniophyllum* (Fig. 233) this function is performed almost entirely by the roots. This plant has no leaves and only a small stem, to which the roots are attached and which bears the flower shoots. The roots, on the other hand, are highly developed and contain chlorophyll.

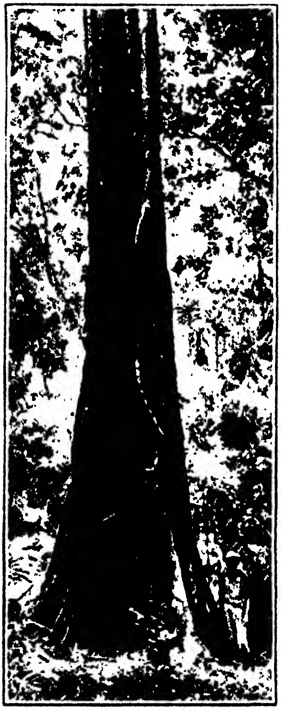


FIG. 237. Roots of strangling fig on a large tree trunk

FIG. 238. An old specimen of strangling fig in which the roots serve as trunks

Support (stem function). In a number of cases, roots take the place of stems in serving as supports. This is the case in the genus *Pandanus* (Fig. 234), where that part of the stem which is near the ground is very small and incapable of supporting the weight of the plant. Large roots grow out from the main stem and serve to brace it; such roots are called *brace roots.* Other roots grow down from the branches and prop them up; such roots are known as *prop roots*. *Rhizophora* (Figs. 235, 281) has similar brace and prop roots. Corn has brace roots. These roots grow out in whorls from the lower nodes and serve to brace the stem of the plant.

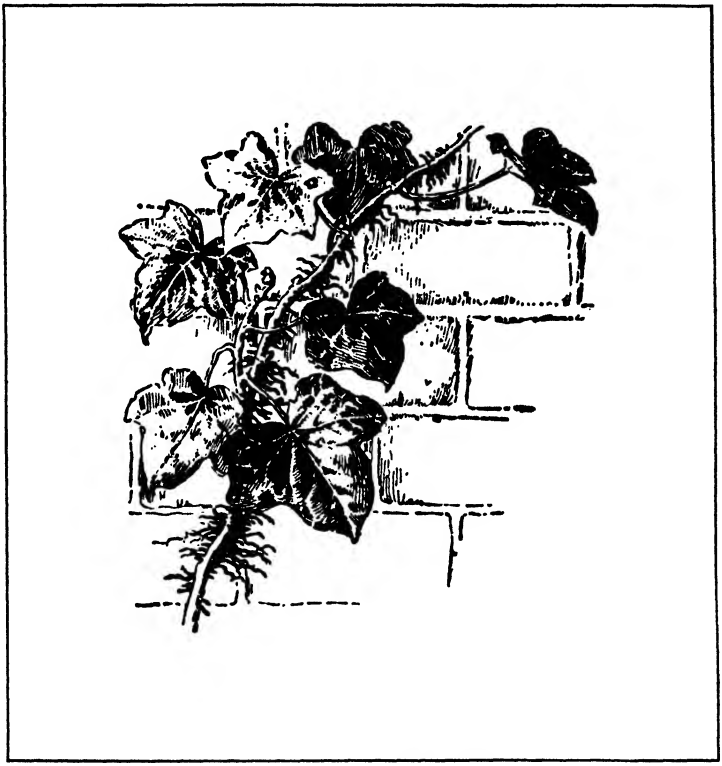


FIG. 239. Aerial adventitious roots of the ivy

Prop roots are conspicuous in many species of the genus *Ficus* (Fig. 236), and particularly in the banyan tree. In the latter case large roots extend down from the larger branches and serve as secondary trunks. As a result one plant may extend over a considerable area and be supported by a large number of prop roots which, from the standpoint of function, may be regarded as additional trunks.

Another very interesting example of supporting roots is afforded by the *strangling figs* of tropical forests. These plants start as epiphytes in the tops of the trees and send down roots that reach the ground (Fig. 237). Branches from these roots grow around the tree and coalesce either with each other or with the main root, until the trunk of the tree is usually enclosed by a network. As this grows and coalesces, it interferes with the growth of the tree, the fig leaves shade the tree, and the roots of the fig interfere with those of the tree. This combination usually results in the death of the tree on which the fig is growing. The meshlike support of the fig continues to grow until it may finally have the appearance of a solid trunk. Usually, however, some of the meshes persist. The final appearance of these figs is greatly influenced by the form and height of the trees on which they start. When they grow on slanting or peculiarly shaped trees, they sometimes assume very fantastic shapes (Fig. 238).

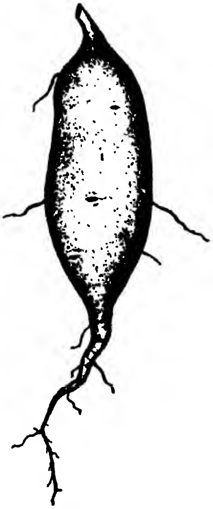


FIG. 240. Root of sweet potato modified for food storage. (× ⅓)

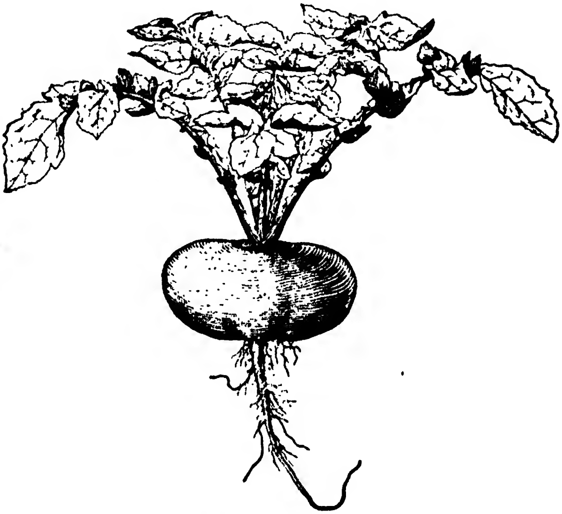


FIG. 241. Enlarged storage root of turnip

Climbing plants may be attached to their supports by means of roots and so be supported by the roots (Figs. 217, 239).

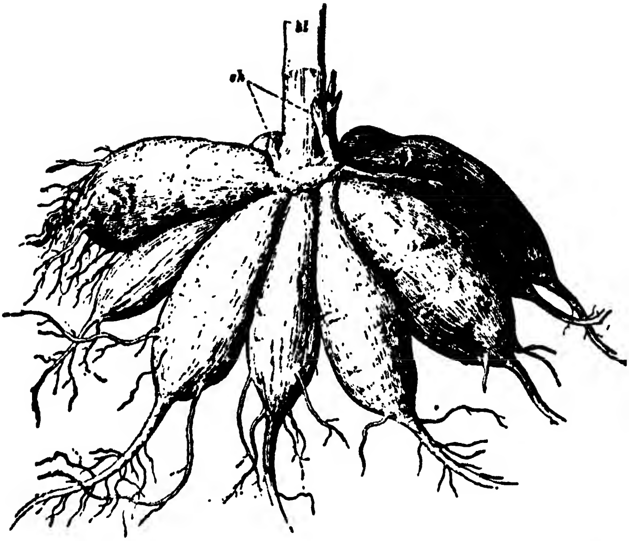


FIG. 242. Clustered, fleshy roots of the dahlia, with much stored plant food, in early spring. (× ¼)

st, remains of last year's stem; *sh*, young shoots beginning to sprout from the upper ends of the roots. (From Bergen and Caldwell, *Practical Botany*)

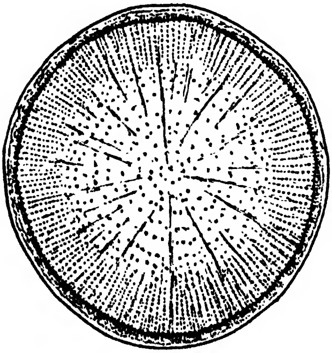


FIG. 243. Cross section of enlarged storage root of turnip

Note that it is composed largely of xylem

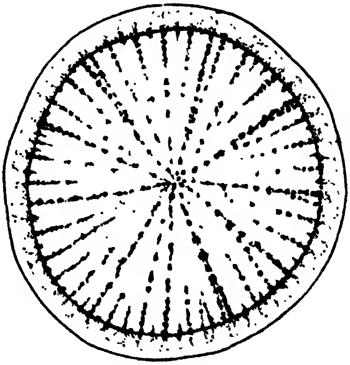


FIG. 244. Cross section of storage root of white radish

The circle inside the root represents the cambium

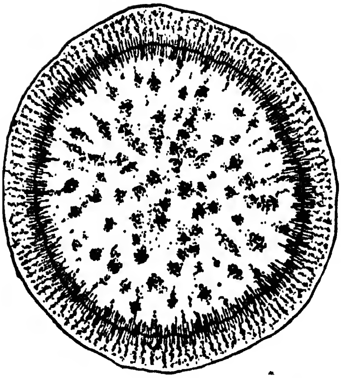


FIG. 245. Cross section of storage root of sweet potato

The circular line in the root represents the cambium

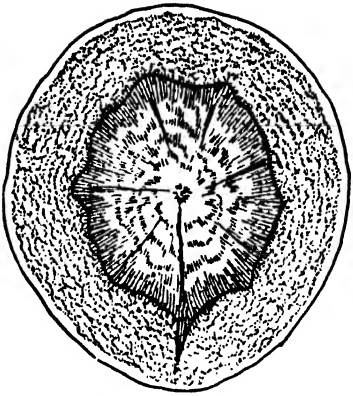


FIG. 246. Cross section of the storage root of carrot

The irregularly circular line in the root represents the cambium

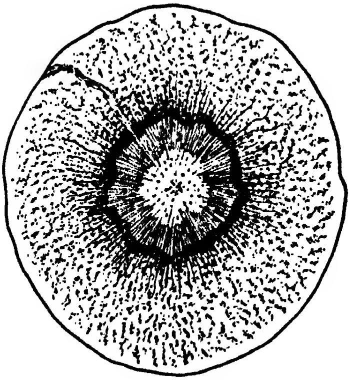


FIG. 247. Cross section of the storage root of parsnip

The irregularly circular line in the root represents the cambium

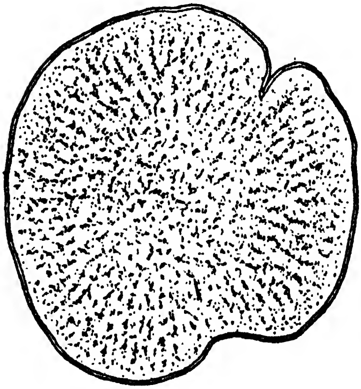


FIG. 248. Cross section of storage root of *Pachyrrhizus erosus*, yam bean or sincamas

Note that the xylem occupies almost the entire cross section and that the cambium is represented by a line near the periphery of the stem

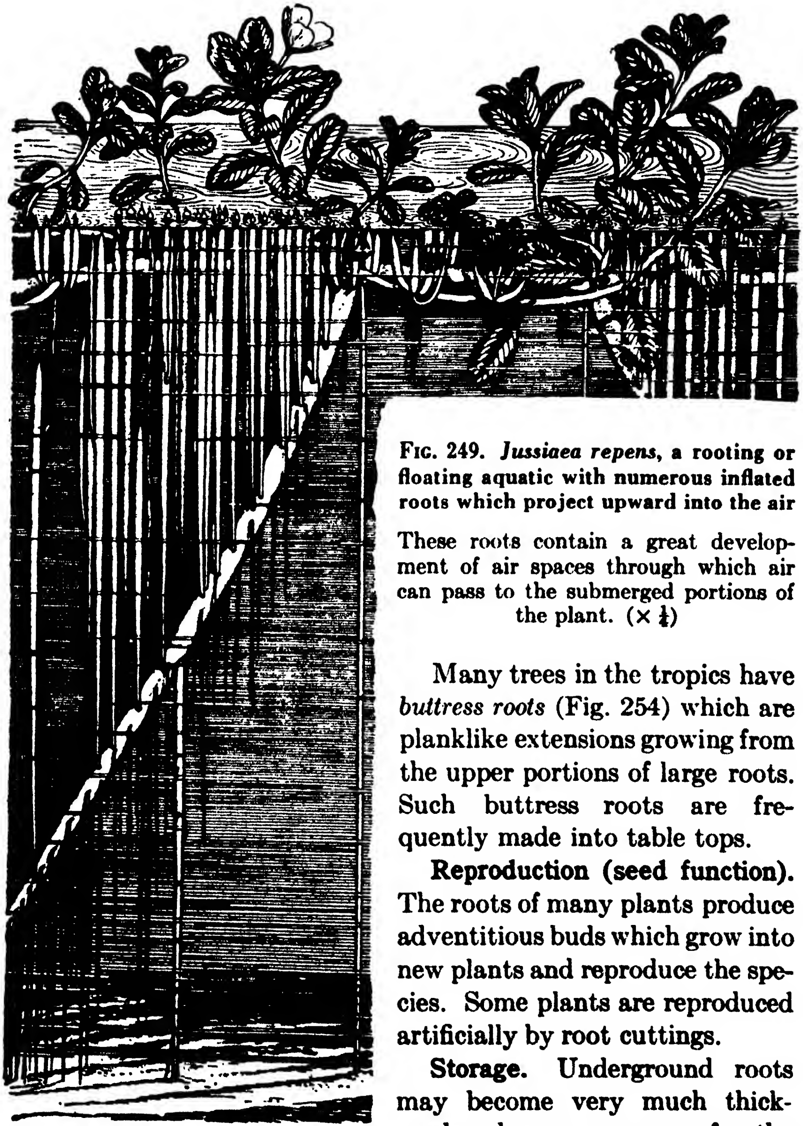


Fig. 249. *Jussiaea repens*, a rooting or floating aquatic with numerous inflated roots which project upward into the air

These roots contain a great development of air spaces through which air can pass to the submerged portions of the plant. (× ¼)

Many trees in the tropics have *buttress roots* (Fig. 254) which are planklike extensions growing from the upper portions of large roots. Such buttress roots are frequently made into table tops.

Reproduction (seed function). The roots of many plants produce adventitious buds which grow into new plants and reproduce the species. Some plants are reproduced artificially by root cuttings.

Storage. Underground roots may become very much thickened and serve as organs for the storage of food. Such is the case in sweet potatoes (Fig. 240), yams, radishes (Fig. 218), turnips (Fig. 241), parsnips, carrots, and dahlias (Fig. 242). Roots may also store water.

In the storage roots the food may be stored largely in the cortex or the xylem region or in both. In turnips (Fig. 243) food is stored largely in the xylem, and the phloem and cortex are relatively narrow. In the radish (Fig. 244) and the sweet potato (Fig. 245) the xylem is also the chief region of food storage, but food is also stored outside the xylem. In the carrot there is a more even distribution between xylem and bark (Fig. 246); while in the parsnip the bark is more prominent than the xylem (Fig. 247). In beets there are alternate layers of xylem and phloem owing to the formation of successive cambiums, as previously explained.

Aeration. Specialized aerating roots are found on a number of plants that grow in submerged soil (Fig. 249). These are particularly prominent in mangrove swamps. Such roots contain a conspicuous development of air space. Oxygen from the atmosphere diffuses into these spaces and then down into the underground root system. The aerating roots extend vertically out of the soil in some mangrove-swamp species (Fig. 282), and also in the bald cypress of the fresh-water swamps of the southeastern part of the United States. In the genus *Rhizophora* (Fig. 235) of the mangrove swamps the aerating roots grow from the trunk and branches and also serve as absorbing roots and as brace and prop roots.

CHAPTER XII

PLANT GEOGRAPHY

The physical characteristics of the vegetation of a given region are largely due to environmental conditions; the systematic relationships depend to a great extent on the past or present geographical connections or barriers. When two regions have been separated for a considerable length of time by barriers such as high mountain chains or wide seas, which it is impossible for most plants to cross, the systematic composition of the vegetation in the two regions will be very different. If the environmental conditions are similar, however, the vegetation of two areas, whether separated or not, is likely to have the same general appearance because in most cases similar external conditions produce associations of plants whose fundamental physical characteristics are much alike. In the present chapter the vegetation of the world will be considered from the standpoint of the physical types of vegetation found in various environments. The most favorable environmental conditions for plant growth are found in those lowland regions of the tropics where moisture is abundant and where there is no pronounced dry season. If from moist tropical lowlands we proceed either to colder latitudes, to higher altitudes, or to drier regions, the environmental conditions become less favorable and the vegetation is less luxuriant. Forests of moist tropical lowlands therefore afford a convenient starting point for a discussion of the vegetation of the world.

Tropical rain forests. Tropical lowlands, where soil conditions are favorable and where there is no distinct dry season or where the dry season is not long and severe, produce very luxuriant forests (Figs. 6, 250). Typically, the forest canopy is composed of three stories characterized by different types of trees. The trees of the top, or dominant, story form a nearly closed canopy which is frequently 60 meters or more in height. The crowns of the second story are beneath those of the dominant story and, like those of

Fig. 250. Rain forest on lower slope of Mount Maquiling, Philippine Islands

Note the different heights of the trees. The feathery leaves belong to climbing palms (rattans) the dominant story, frequently form a nearly closed canopy. The trees of the third, or lowest, story are usually small and slender and have small open crowns. The presence of these three stories of different trees is not usually evident on casual observation, for the composition of all the stories is very complex and few of the trees present any striking peculiarities. Moreover, smaller trees of a higher story always occur in a lower story as well as between the different stories, while the different species of a story have different heights. Erect palms are frequently numerous in the lower stories but are seldom a prominent part of the vegetation.

FIG. 251. Climbing palms (rattans) in Philippine rain forest

Beneath the tree stories there is a ground covering, the composition of which varies in different situations. In rather dry areas, particularly on ridges, it may consist largely of woody plants, while in moist situations, especially in ravines, herbs are abundant. Among the latter, ferns are frequently prominent.

Large vines are always conspicuous in moist tropical forests. Among these are the climbing palms, bamboos, and aroids. In the Malayan region the long, feathery leaves of rattans (climbing palms chiefly of the genus *Calamus*) are particularly striking (Figs. 95, 251). Dicotyledonous vines are conspicuous chiefly as large cables hanging from the crowns of the tall trees.

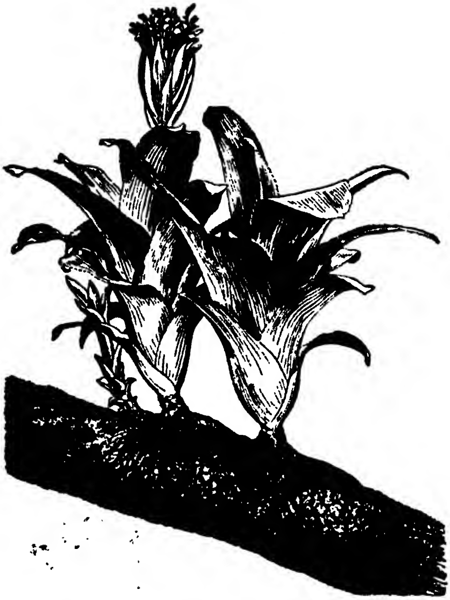


Fig. 252. An epiphytic bromeliad (*Billbergia*)

Note that the leaves form urn-shaped cups for collecting water, which is absorbed by absorbing hairs on the leaves. (× $\frac{1}{10}$)

Epiphytic vegetation is abundant but is confined chiefly to the larger branches of dominant trees, where it frequently forms striking aerial gardens. The conspicuous epiphytes are ferns and flowering plants, orchids (Fig. 2) being very numerous. Bromeliads (Fig. 252) are conspicuous in the American tropics. In general the epiphytes have a xerophytic structure; many of them contain abundant water-storing tissue.

The most striking feature of moist tropical forests is the great development of foliage, which is usually continuous from the ground covering to the top of the forests. Although such a forest consists chiefly of large trees, the thing that strikes the eye is not the gigantic trunks but rather the foliage which hides the trunks (Fig. 253). In some tropical forests the canopy is exceedingly dense and there is little development of undergrowth and ground covering. Here the trunks of the trees stand out as gigantic columns. The great luxuriance of tropical rain forests is explained by the fact that moisture, temperature, and light are continuously favorable. The same favorable conditions, particularly in regard to moisture, are responsible for the great development of epiphytes. Large epiphytes are more dependent on a continuous supply of atmospheric moisture than the terrestrial plants, and they cannot stand prolonged periods of adverse moisture conditions, whether these are due to lack of atmospheric moisture or to cold. In keeping with the great luxuriance of the vegetation, the number of species of trees, vines, and epiphytes in moist tropical forests is greater than in less favored regions. More than a hundred species of trees have been counted on a quarter of a hectare.

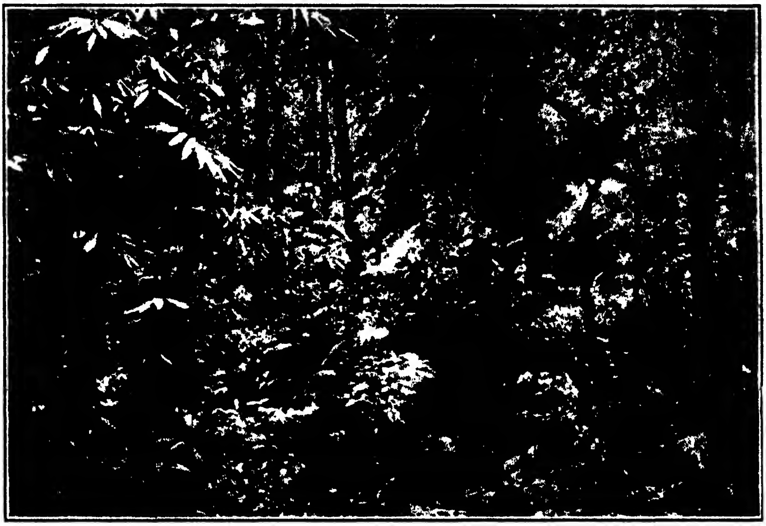


Fig. 253. View in rain forest on lower slope of Mount Maquiling, Philippine Islands

Note the density of the foliage, which hides the large tree trunks

Flowers are usually inconspicuous in the forest. This is due to the fact that the production of flowers is extended over a long period instead of being crowded into a short flowering season, and to the fact that as one views the canopy from below the flowers are largely hidden by the foliage.

Tropical forests have been considered as the home of bizarre plants. If the large number of species found in tropical forests is taken into consideration, the number of curious species in the tropics is probably no greater in proportion to the total number present than in other regions. If by *curious* is meant "specialized," or different from the great majority of plants, then certainly desert vegetation is much more bizarre than is the vegetation of the moist tropics. The vegetation of the temperate zone, with its deciduous leaves, annual rings of growth, highly specialized bud scales, and other features connected with the winter season, is much more specialized than is tropical vegetation. Moist tropical vegetation contains a greater wealth of forms than is found in less favored localities. Among these forms are many, such as climbing palms (Figs. 95, 251) and begonias, not found elsewhere. Such plants are hardly more peculiar in themselves than are other plants. That such plants have been described as peculiar is largely because they are unfamiliar in the native homes of those who have described them.

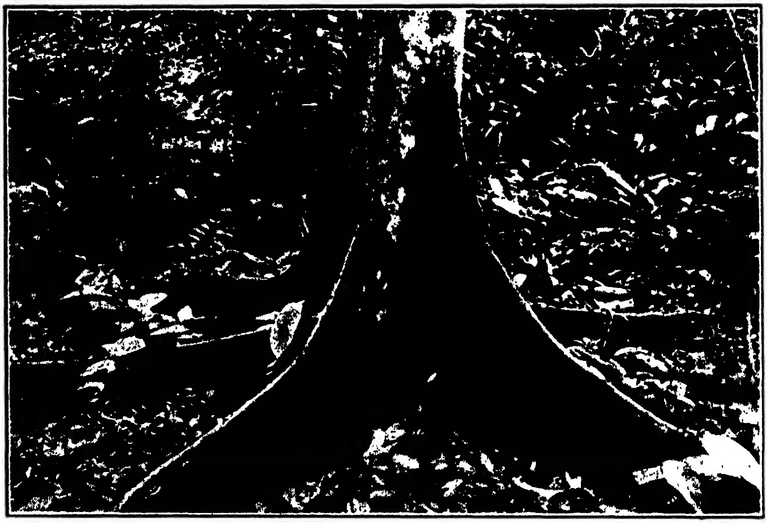


FIG. 254. Base of a tree trunk showing buttress roots

A number of interesting types of plants do, however, occur in moist tropical forests (Fig. 65). Strangling figs (Figs. 237, 238) present a very peculiar appearance and are sometimes numerous. Trees with large buttress roots are rather common (Fig. 254). In a considerable number of species, flowers and fruits occur on the trunks and the large branches, but such species constitute a very small, inconspicuous proportion of all the trees present. Humus-collecting epiphytic ferns (Figs. 104, 255) are sometimes abundant. Curious plants of the Malayan region also include large flowering parasites (Figs. 7, 189) and plants that have swollen stems (Figs. 214, 215) which are inhabited by ants, but such plants are usually rare and never form a conspicuous part of the vegetation.

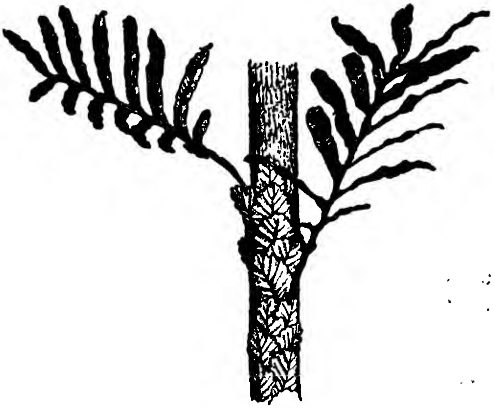


FIG. 255. *Drynaria*, an epiphytic fern which has small humus-gathering leaves and large leaves which carry on photosynthesis and produce spores. (× $\frac{1}{18}$)

Subtropical and warm temperate rain forests. In subtropical and warm temperate regions, where rainfall is abundant and well distributed through all parts of the year, there are evergreen forests. Near the tropics these are similar to the tropical rain forests, but as colder latitudes are reached the forests begin to partake more of the characteristics of the deciduous forests of the cold temperate regions. Subtropical and warm temperate forests are generally of lower stature than are the tropical rain forests, and they have fewer woody vines and epiphytes. Subtropical or warm temperate forests occur in southern Japan, Florida, northern Mexico, New Zealand, southeastern Australia, and parts of South America. In southeastern Australia they are found in gullies and valleys, and their luxuriance is due more to subterranean water than to rain. The rain forests of Australia and New Zealand are characterized by a great abundance of tree ferns.

Cold temperate deciduous forests. In cold temperate regions there are two classes of forests: the deciduous broad-leaved forests (Fig. 256) and the evergreen needle-leaved, or coniferous, forests (Fig. 257). The cold winter season, from a physiological standpoint, is a dry period, owing to the fact that low temperature hinders the absorption of water by the roots. In broad-leaved forests the lessened ability of the roots to absorb water is counterbalanced by the loss of the leaves, and so the trees are leafless during the winter season (Fig. 258). These deciduous forests are very much less luxuriant than the tropical rain forests. The trees form only a single story, and when this is well developed there is scanty development of undershrubs and herbs. The space under the main canopy is therefore open (Fig. 259), instead of being densely filled as is the case in most of the tropical rain forests. Climbing vines are scarce and confined chiefly to the edges of the forests. Epiphytes are also scanty and, except in the warmer parts of temperate zones, consist only of bryophytes, lichens, and algæ. The best development of deciduous forests occurs in the eastern part of the United States.

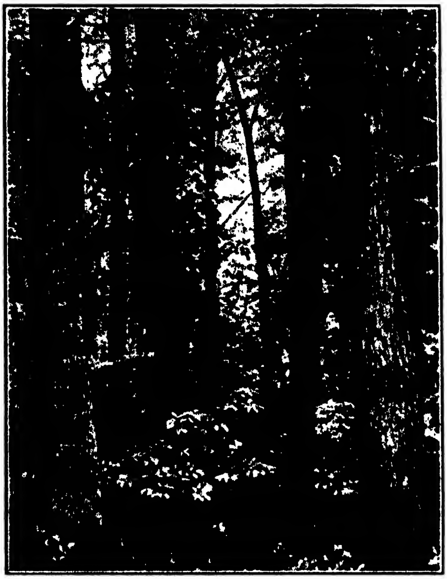


FIG. 256. Deciduous forest in northeastern part of the United States

Photograph by Dr. George E. Nichols

During the winter season the buds of most of the species are protected by specialized scales which prevent the buds from being desiccated (Fig. 114). The time of growth and development of the leaves is determined by the seasons. The winter buds contain the flowers and leaves of the coming spring and summer. The flowers usually expand at the beginning of the growing season, before the leaves appear or are fully developed. The leaf buds open and the leaves expand very rapidly. The foliage is fully developed early in the season, and the expansion of new leaves then ceases. During the latter part of the season the buds that will expand during the next spring are formed, and food material, which will make possible rapid growth in the spring, is stored in the stems.

The expansion of the foliage early in the season is of great advantage, as it allows all the leaves to function for the greatest possible length of time. The early appearance of flowers allows time for the development of the fruit and at the same time facilitates pollination, as both wind and insects have freer access to the flowers in a leafless forest than in one in full foliage.

One of the most striking characteristics of the forests is the behavior of small perennial herbs with persistent underground portions which send up flowers and leaves before the appearance of the leaves on the trees and so make use of the bright light which reaches them before they are shaded by the foliage of the trees over them. The aerial parts of many of these plants disappear early in the season.

The changes in appearance which the forests undergo with the changing seasons are very striking. During the winter the trees are leafless and only a portion of the herbaceous vegetation retains its foliage. In the spring early-flowering herbs carpet the ground and flower profusely, while shrubs and trees burst into bloom. Most of the trees are wind-pollinated and have inconspicuous flowers, but some of them have conspicuous insect-pollinated flowers. At this time the great array of blossoms

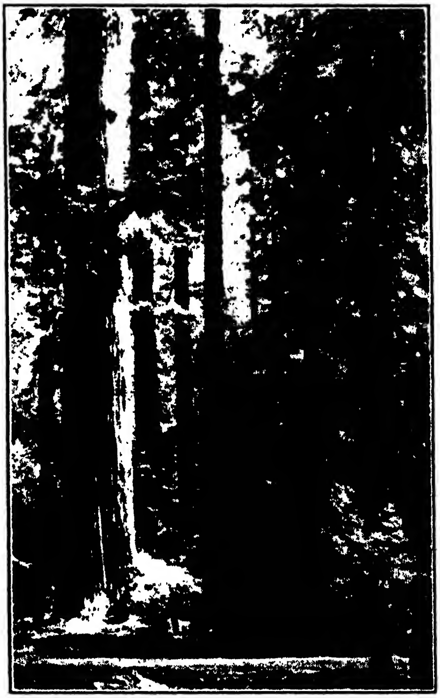


Fig. 257. **Redwood forest, Humboldt County, California**

Photograph by Dr. William S. Copper

renders the forest an object of great beauty. In summer the foliage predominates and flowers are scarce. In autumn, before the trees shed their foliage, the leaves of many of them change from green to brilliant shades of red, yellow, and brown, and again the forest is strikingly beautiful. As the brightly colored leaves fall, the forest enters the period of winter rest.

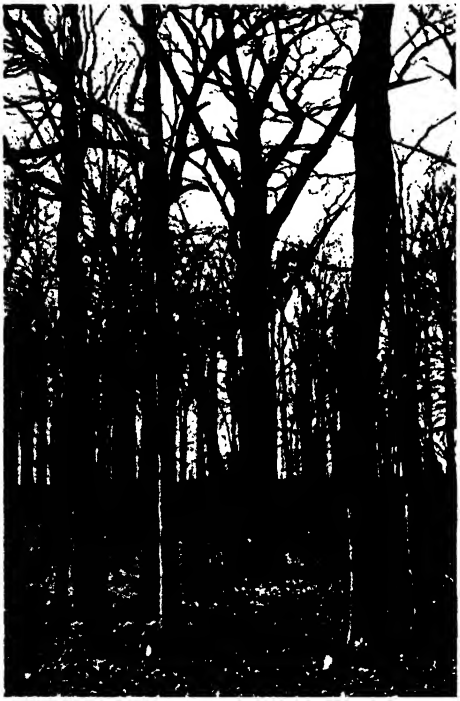


Fig. 258. Leafless condition of a deciduous forest in the northeastern part of the United States

Coniferous forests. The evergreen coniferous trees of the north temperate zone are adapted to withstand the desiccating effects of winter by having xerophytic needlelike or scalelike leaves (Figs. 991, 996). The xerophytic structure of the leaves enables the trees to retain their foliage throughout the winter, the leaves of most species remaining on the trees for a number of years. The retention of the foliage throughout the year has the advantage that the leaves can carry on photosynthesis whenever conditions are favorable, and the same leaves can function for several seasons.

Undergrowth is usually less dense in a well-developed temperate-zone coniferous forest than in a deciduous one. This is due in part to the fact that in the coniferous forests there is no season during which the undergrowth is not shaded by the foliage of the trees, and in part to the fact that a carpet of slowly decaying, dry, resinous leaves hinders the establishment of seedlings.

Vast areas in the north temperate zone are covered by coniferous forests (Figs. 990, 257, 260). These are well developed in Europe, Siberia, and Canada, and in the northern, western, and southeastern portions of the United States. The northern boundary coincides everywhere with the limit of tree growth. The largest stands of timber in the world are found in the coniferous forests which appear on the western coast of the United States.

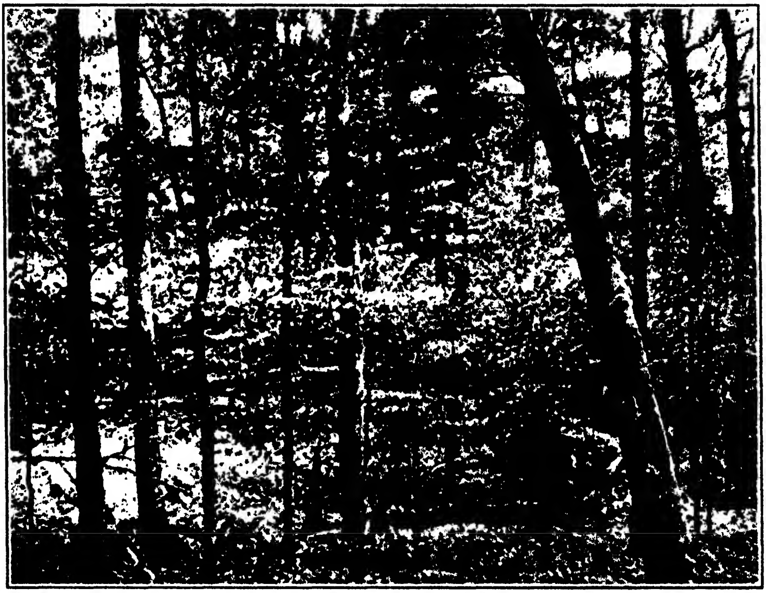


FIG. 259. Summer condition of a deciduous forest in the northeastern part of the United States

Photograph by Dr. George E. Nichols

Tundra. From the standpoint of plant geography the boundary of the arctic region may be considered as the place where the last stunted trees disappear (Figs. 261, 262). This may be on either side of the arctic circle. North of this limit, where ice does not cover the ground tundra dominates the arctic region. The growth is usually open and always dwarf, and mosses and lichens predominate. In favored situations there may be patches of meadows or dwarfed shrubs. The growing season is very short, about two months, so that the spermatophytes rapidly pass through the stages from flowering to fruiting. One of the most striking characteristics of the tundra is the abundance and large size of the flowers as contrasted with the small, short stems (Fig. 263).

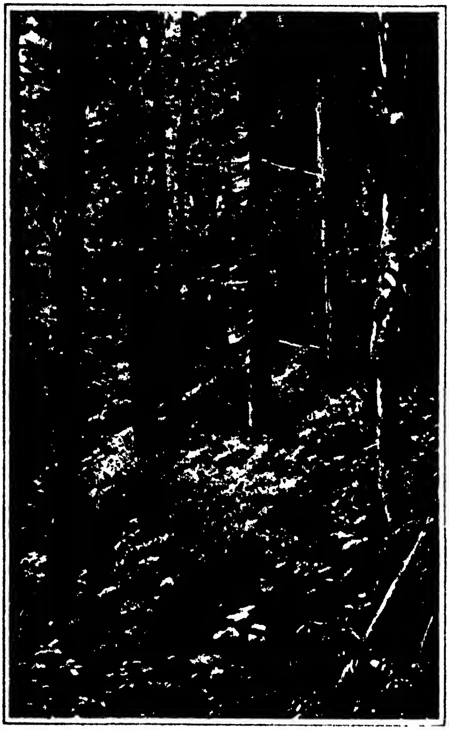


FIG. 260. Interior of coniferous forest, Taku Inlet, Alaska

The trees are *Picea sitchensis* and *Tsuga heterophylla*. Photograph by Dr. William S. Cooper

Mountain vegetation. The vegetation at different altitudes on mountains is profoundly affected by the changes in the climate at different elevations. With rising altitudes the temperature steadily decreases until, if the mountain is sufficiently high, there is a perpetual cap of snow. Rainfall is usually heavier on the lower slopes of mountains than in the surrounding lowlands. This is due to the fact that as the warm air from the lowland is forced up the mountainside it cools, with the result that its water-holding capacity is lessened and the consequent excess of water in the atmosphere forms clouds, which frequently give rise to rain. The amount of rainfall increases up to a certain altitude, and then decreases because as the air continues to lose water in the form of rain it retains less and less moisture. The large rainfall at low and medium altitudes on mountains frequently results in a more luxuriant vegetation in these situations than in the neighboring drier lowlands. The greater luxuriance of the vegetation at low and medium altitudes on mountains is particularly striking when

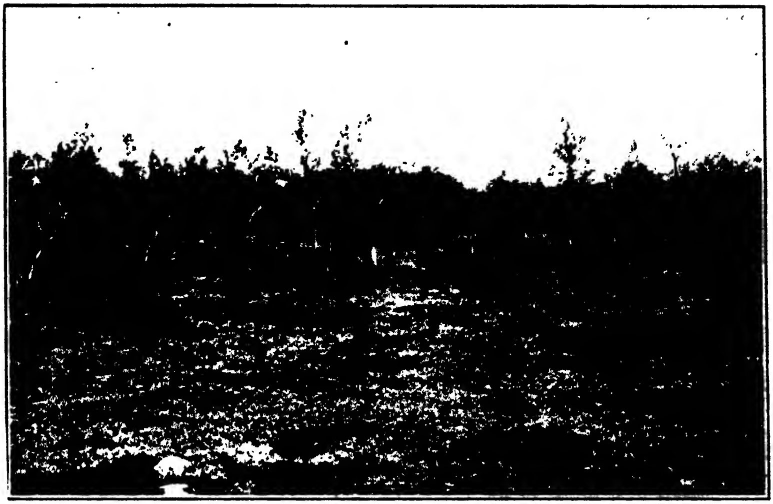


FIG. 261. Birch forest with lichens, Lapland

Photograph by C. G. Alm

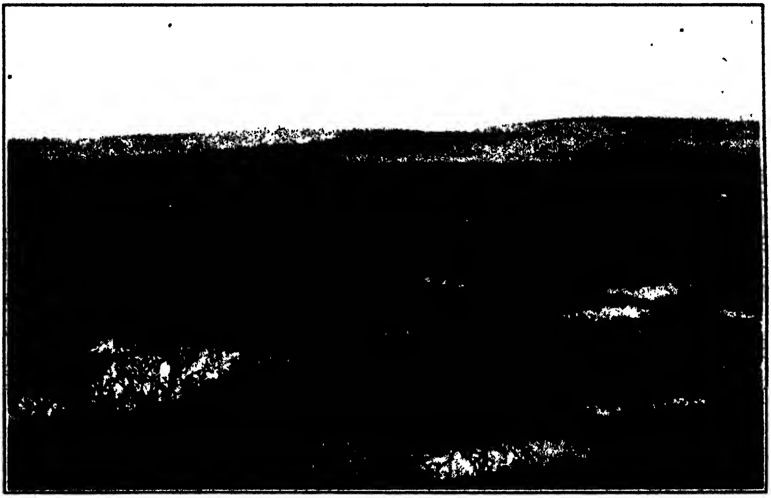


FIG. 262. Dwarf birch heath, Lapland

Photograph by C. G. Alm

the mountains rise from a dry or desert region. This is seen in Arizona, where the country around the mountains, and even the lower slopes of the mountains themselves, produce only desert vegetation, while at higher altitudes there occur rather luxuriant coniferous forests.

On mountains the height of the forests decreases with rising elevation. At low and medium altitudes a greater luxuriance sometimes results from increased rainfall, but with this exception the height of the forests decreases until, frequently, the forest passes into elfin wood, which consists of stunted and twisted trees (Fig. 264). Above the elfin wood there is often an area of dwarf shrubs, which in turn gives way to alpine meadow (Figs. 265, 266). This consists of a short, xerophytic, matted vegetation of grasses or dicotyledonous herbs, or both. Where conditions are favorable this vegetation extends to the region of perpetual snow. As in the arctic tundra, the flowers of the alpine meadow are large in comparison with the dwarf plants (Fig. 266).

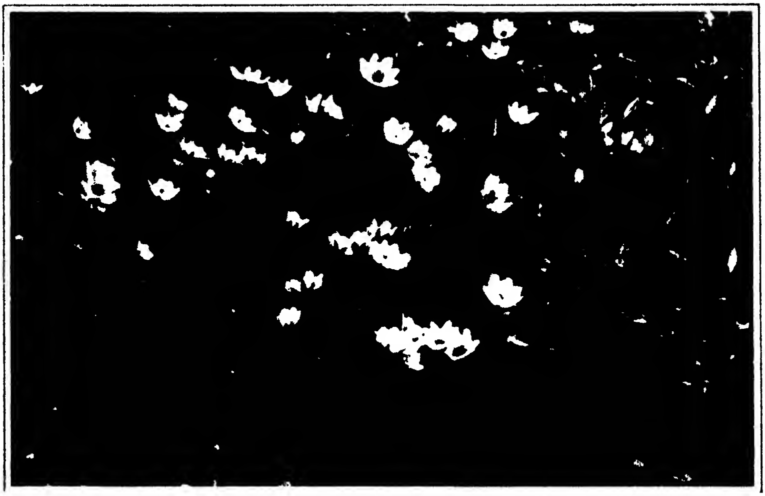


Fig. 263. *Dryas octopetala* **in flower in Lapland**

Photograph by C. G. Alm

On moist tropical mountains the three-storied rain forests give way to a lower forest, which often consists of two stories, and

Fig. 264. ***Pinus flexilis*** **at timber line, Longs Peak, Colorado**

Photograph by Dr. William S. Cooper

Fig. 265. Alpine meadow invading glaciated rock surface, Glacier Gorge, Longs Peak, Colorado

Photograph by Dr. William S. Cooper

which in many respects resembles the subtropical rain forest (Figs. 267, 268). It is less rich in species of trees than is the tropical rain forest, and contains fewer woody vines and usually a smaller percentage of phanerogamic epiphytes, while epiphytic mosses and liverworts are more numerous. In general, epiphytic vegetation is more luxuriant (Fig. 269) than in the three-storied rain forest. Above the two-storied forest there is an elfin wood consisting of a single story of twisted trees (Figs. 270, 271). Usually the trunks and branches of the trees of the elfin wood (Figs. 271, 272), and sometimes those of the two-storied forest at higher altitudes, are densely covered with a thick mat of mosses and liverworts. The mosses and liverworts not only cover the trunks and branches but also hang down in graceful festoons (Fig. 271). In the mosses and liverworts grow numerous ferns and a considerable number of flowering plants.

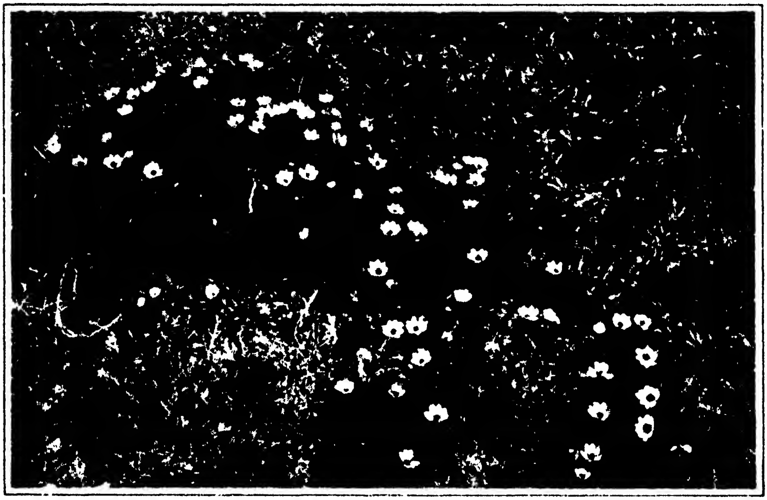


Fig. 266. Alpine meadow near Mount Robson, British Columbia

Compare with Fig. 263. Photograph by Dr. William S. Cooper

Flowers of epiphytes, vines, and trees are usually numerous in this mossy forest, and, owing to the low stature of the trees, are conspicuous. The small size of the trees and their twisted form,

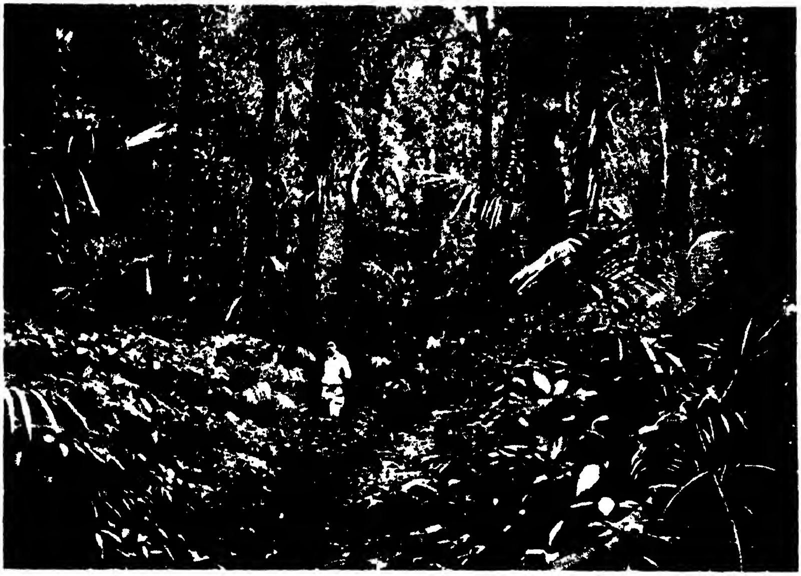


FIG. 267. Two-storied forest on Mount Maquiling, Philippine Islands, at an elevation of seven hundred and forty meters

FIG. 268. Another two-storied forest on Mount Maquiling, Philippine Islands, at an elevation of seven hundred and forty meters

the thick mantles and festoons of mosses and liverworts, and the numerous blossoms give the mossy forest a weird yet attractive appearance and make it one of the most striking types of vegetation found in the tropics.

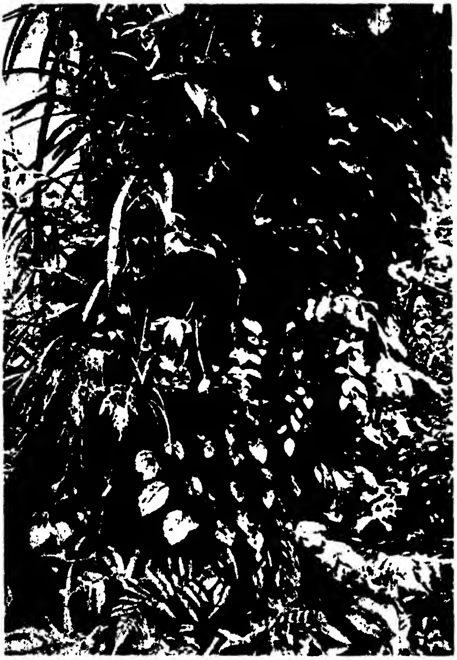


FIG. 269. Epiphytes on trunk near the upper limit of two-storied forest on Mount Maquiling, Philippine Islands

Monsoon forests. In the tropics, regions with one or two pronounced dry seasons of several months' duration are much greater in extent than are those with a constantly humid climate. A seasonal climate is particularly characteristic of the interior of continents. Where the rainfall is abundant during the wet season well-developed forests occur, but the vegetation is not so luxuriant as it is in the constantly moist regions. During the dry season much of the foliage is shed, the degree of defoliation depending on the severity of the season. Over large areas the loss of leaves is never uniform, as along watercourses trees keep their foliage throughout the year. Except when the dry season is extreme, occasional evergreen trees occur. During the dry season the monsoon forests do not present as lifeless an aspect as do deciduous temperate forests in the cold season, as the dry season is pre-eminently the time of flowering.

Monsoon forests resemble the deciduous forests in temperate regions in being of lower stature than tropical rain forests. They are also similar to the temperate-zone deciduous forests, and dif-

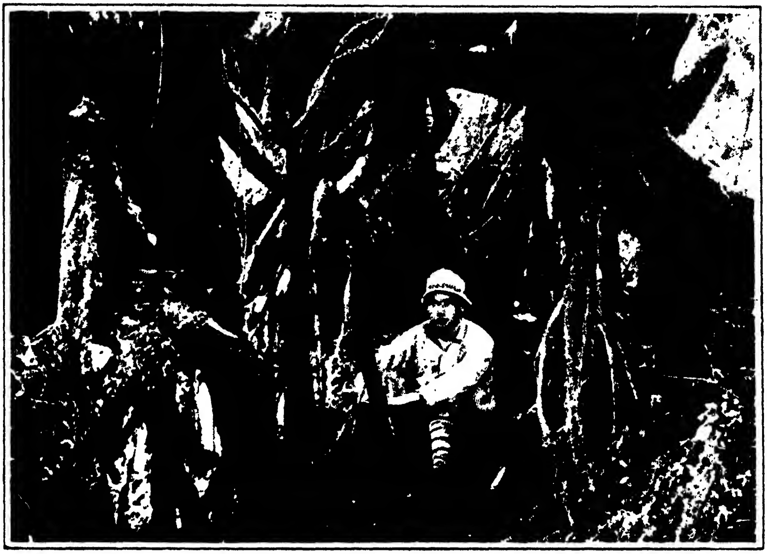


Fig. 270. Lower part of twisted tree with many aerial roots in mossy elfin forest near summit of Mount Maquiling, Philippine Islands

Fig. 271. View of mossy elfin forest near summit of Mount Maquiling

The trunks, branches, and aerial roots are covered with festoons of mosses ferent from tropical rain forests, in that the trees have thick bark and annual rings of growth in the wood, and lack buttressed roots.

Xerophilous forests. Dry tropical and subtropical regions which are not dry enough to produce deserts support either xerophilous forests (Figs. 1040, 273) or grassland. The xerophilous forests may be either evergreen or deciduous. The trees are usually of low stature as compared with rain or monsoon forests, but there are exceptions, the giant eucalyptus forests of western Australia being pronounced xerophilous forests. The vegetation is more open than in rain forests or monsoon forests, and the leaves are much more xerophytic than in the latter types. The xerophilous forests often grade into bush land (Fig. 274), grassland, or desert.

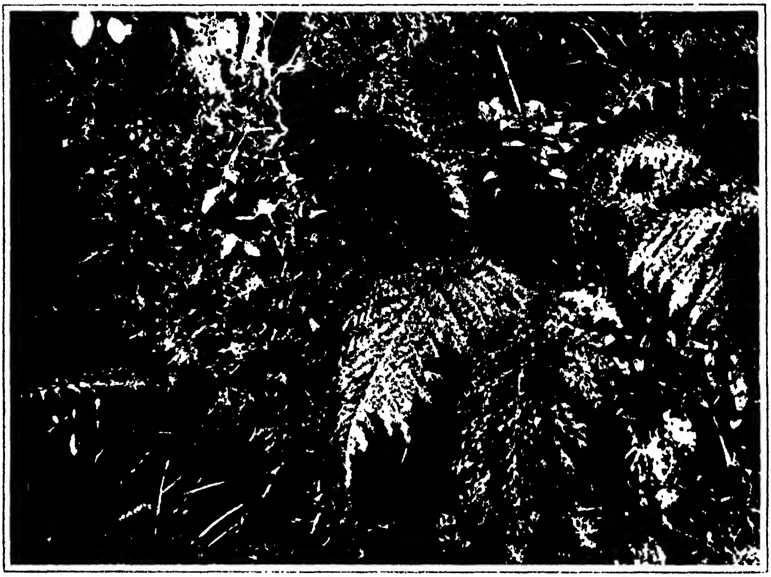


FIG. 272. Growth of mosses and a filmy fern on a trunk in mossy elfin forest near summit of Mount Maquiling, Philippine Islands

Grassland. Grassland in tropical and subtropical regions usually takes the form of savanna, in which widely spaced trees occur with the grass (Fig. 275). In temperate regions grasslands are usually without trees except along watercourses. In the United

States the more moist grassland, or prairie, is excellent for raising grain, while the drier grassland, or plain, is good for grazing.

In many cases extensive grasslands are due to the interference of man rather than to natural conditions. In temperate regions meadows are frequently produced as a result of cultivation. In the Malay Archipelago large tracts of rank waste grasslands are due to periodic fires which have followed the removal of the original forests. The fires destroy dicotyledonous plants but do not appreciably damage the underground rhizomes of the grasses. Similarly,

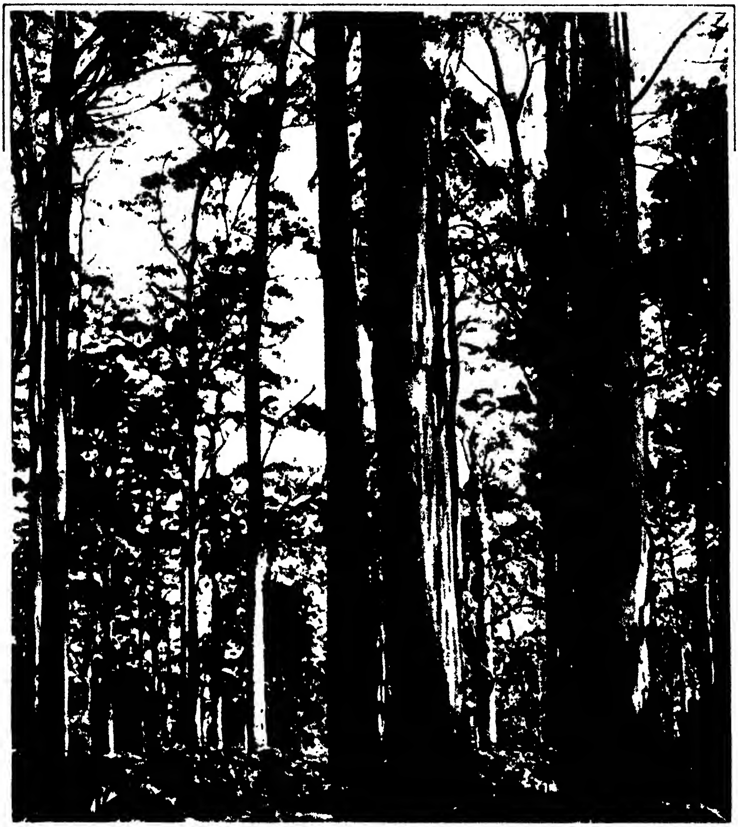


FIG. 273. Sclerophyllous forest in Australia in a region with an annual rainfall of thirty to forty inches

fires are frequently responsible for the presence of grasslands in temperate areas.

Deserts. Areas which have a very slight rainfall and are covered by a scanty growth of scattered plants are known as deserts (Figs. 84, 276). The largest area stretches across Africa into southeastern Asia. In Africa it is called the Sahara Desert, and in Asia it is called the Arabian Desert. The next largest area includes most of central Asia. Large desert areas occur in central Australia and in Mexico and the western part of the United States, while small areas are found in southwestern Africa and South America.

FIG. 274. Bush land in Australia in a region with an annual rainfall of ten to thirty inches

Photograph by Professor D. A. Herbert

Deserts are characterized by an open growth of comparatively small plants many of which are thorny (Figs. 84, 277). Plants of desert regions are adapted in various ways to withstand adverse conditions. Some, particularly shrubs and shrubby trees, have long roots that reach down to subterranean water. The cacti have roots that spread near the surface of the soil; when the soil is

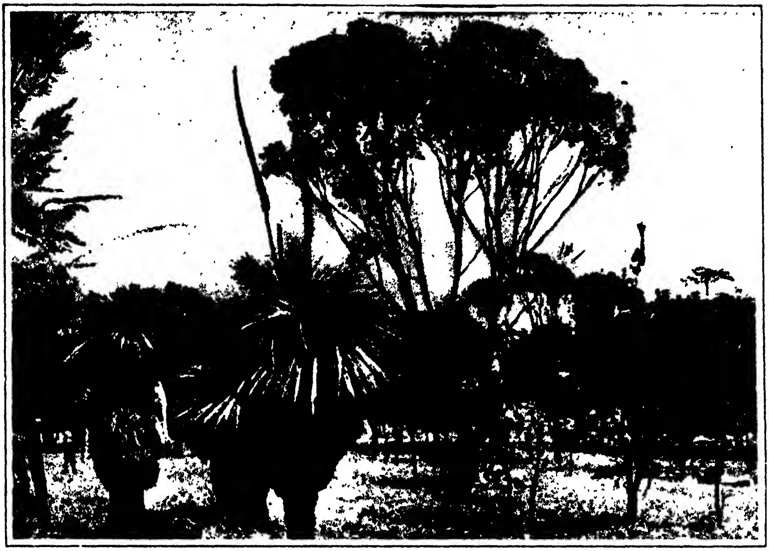


FIG. 275. Savanna in Australia under annual rainfall of ten to thirty inches
Photograph by Professor D. A. Herbert

FIG. 276. Desert region in Arizona
Photograph by Dr. Forest Shreve

wet, considerable quantities of water are absorbed by the extensive root system and then stored in the enlarged stems. Deserts usually have a short rainy season when conditions are fairly favorable to vegetation and during which annuals spring up and pass through their whole development. Such annuals do not have a xerophytic structure. Other plants, with perennial underground portions, send up aerial shoots which disappear after the moist period. Some of the shrubs are leafless or have greatly reduced scale leaves; others have small xerophytic evergreen leaves; still others are deciduous and have mesophytic leaves during the rainy period.

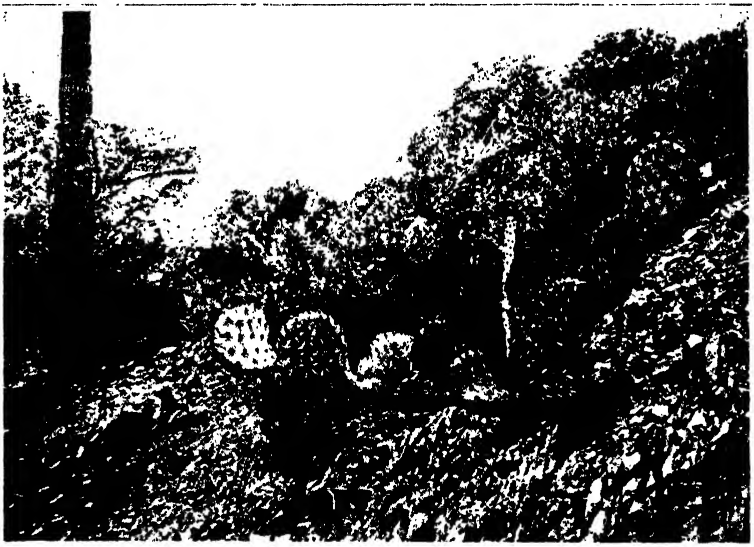


Fig. 277. Arizona desert with large *Opuntia*

Photograph by Dr. Forest Shreve

The appearance of deserts varies greatly according to the kinds of plants found in them. In many places the plants are largely shrubs (Fig. 278), while in other regions succulents are conspicuous (Figs. 277, 279). In parts of the American desert cacti predominate, while in parts of Africa, particularly in the south, there are numerous euphorbias with a general appearance similar to that of certain cacti.

The appearance of deserts also changes according to the seasons: during a dry period the vegetation is very scanty and has a gray or rather dirty green color, while in the rainy period the vegetation is much more luxuriant owing to the presence of the annuals and of the mesophytic foliage on the deciduous perennials. At the same time flowers are frequently found to be very numerous.

FIG. 278. Scene in Arizona desert

Photograph by Dr. Forest Shreve

Marine vegetation. In seas, floating microscopic algæ are numerous, and among them diatoms are prominent. These microscopic floating plants are the chief source of food for marine animals.

Macroscopic marine plants are either algæ or angiosperms, the algæ predominating. The angiosperms are grasslike plants but not true grasses, and grow rooted in sandy or muddy bottoms of calm, shallow bays. Macroscopic algæ are most abundant on rocky coasts; for the most part they are attached to the rocks, but they may be attached to other objects, such as shells or other algæ. Algæ occur not only below the level of low tide but between tide levels, and in cold temperate regions on rocky coasts the development of algæ between tide levels is very luxuriant. Macroscopic algæ range in size from small plants which are hardly visible to large ones many meters in length.

Fresh-water vegetation. In fresh water, as in salt water, microscopic floating algæ are very abundant, and among them diatoms are numerous. The macroscopic vegetation differs very greatly from that of salt water, as flowering plants predominate over the algæ, while the algæ are small as compared with those of salt water. The macroscopic plants may be divided into three general classes: submerged plants, rooted plants with floating leaves, and floating plants.

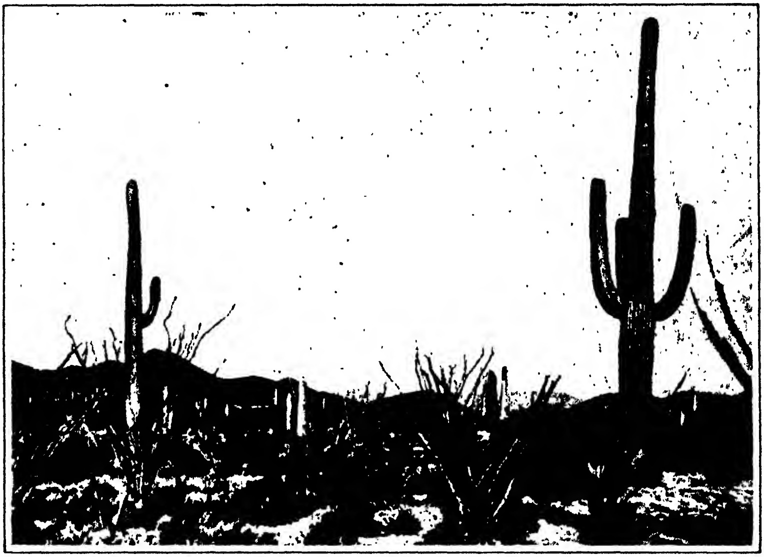


FIG. 279. Scene in Arizona desert

Note the conspicuous giant cacti (*Carnegiea*). Photograph by Dr. Forest Shreve

In general, plants which are entirely submerged grow in deeper water than do those with floating leaves. The conducting and strengthening tissues are very poorly developed in submerged plants. As they float in the water, they do not need strengthening tissue to the same extent that land plants do; and as they do not transpire, there is no necessity for any considerable development of water-conducting tissue. The leaves are thin and in many cases are finely divided, thus exposing large surfaces for the absorption of materials.

Plants with floating leaves have a conspicuous development of air spaces (Fig. 74). These serve as an aerating system for the diffusion of oxygen from the leaves to the roots. Moreover, the air spaces in the leaves are of assistance in enabling the leaves to float on the surface of the water.

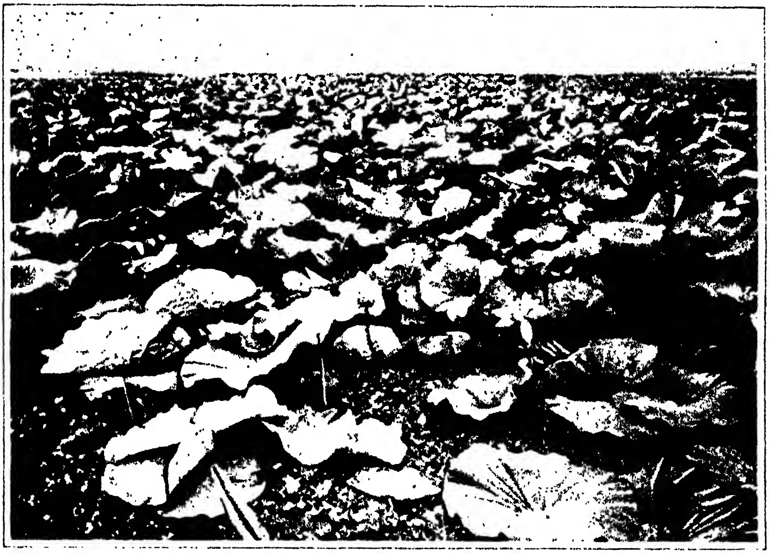


FIG. 280. Lotus (*Nelumbium nelumbo*) projecting out of the water, and *Pistia stratiotes* floating on the water, in Laguna de Bay, Philippine Islands

Floating plants of cold temperate countries are all of small size, but they may be abundant enough to cover the surfaces of small ponds. In warmer regions floating plants reach larger size (Fig. 5), and the water hyacinth (Fig. 97) may obstruct navigation in sluggish streams. Floating plants are provided with well-developed air spaces (Fig. 96), which make the plants buoyant and at the same time serve as passageways in which oxygen can diffuse to the roots. The roots hang down in the water and serve as a counterpoise which helps to keep the plant right side up.

Swamp vegetation. Around the edges of quiet bodies of fresh water, and in shallower water than that in which plants with floating leaves occur, there is often a conspicuous development of swamp composed largely of erect plants (often monocotyledonous) with roots under water or in saturated soil and with shoots extending into the air (Fig. 280). Such plants contain conspicuous air passages for the aeration of the roots. In other cases the shallow water is occupied by a growth of shrubs or trees. Salt-water swamps in temperate regions are occupied by a reedlike growth consisting largely of monocotyledonous plants. In the tropics mangrove-swamp forests are formed on mud flats which are exposed at low tide and at high tide are covered by salt water.

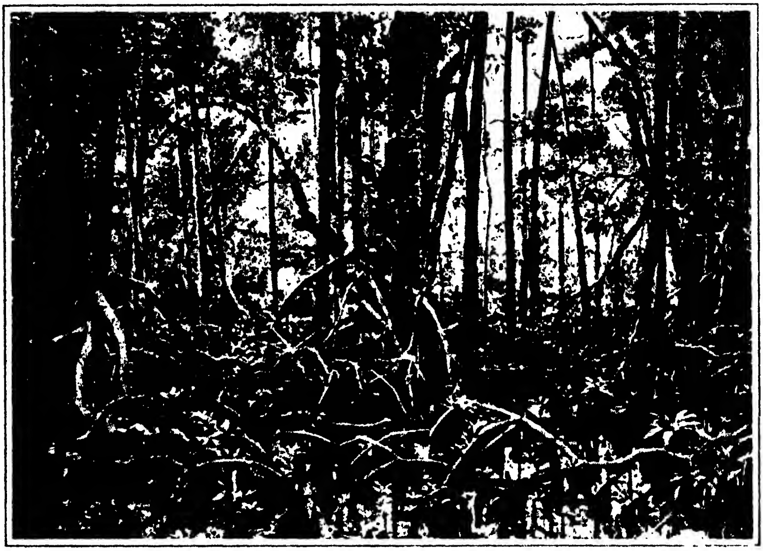


Fig. 281. Interior of Philippine mangrove swamp at low tide

Note the aerating prop roots of *Rhizophora* and the erect aerating roots which project upward out of the mud

Mangrove-swamp forests. The term *mangrove-swamp forest* is applied to the type of forest occurring on tidal flats along tropical seacoasts (Figs. 235, 281). The conditions most favorable to their development are found in quiet bays into which flow large rivers whose lower reaches have little fall. The descending waters of the rivers are checked when they meet tidewater, and deposit their sediment in the form of broad flats or deltas near the mouths of the rivers. These flats are usually cut by a network of channels through which the advancing and receding water of the sea moves.

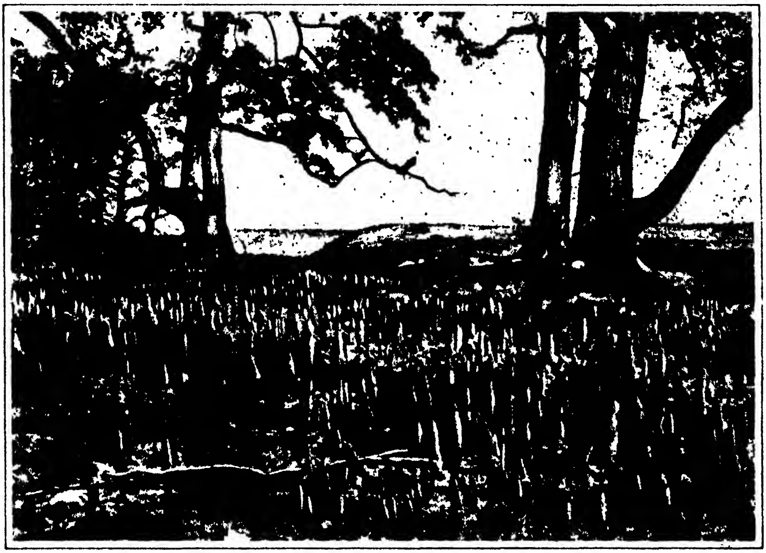


FIG. 282. Aerating roots of *Sonneratia caseolaris* in Philippine mangrove swamp

At extreme low tide the flats are exposed, and often even the larger channels are dry. On these mud flats the trees which form the mangrove vegetation find conditions favorable to their development; and as the seeds or seedlings of these species are distributed by water and can be transported for long distances without injury, the formation of flats and their seeding are almost simultaneous. When conditions are favorable, new flats are formed beyond the old, and the forest advances year by year. The mangrove forests may contain trees more than a meter in diameter, and when fully stocked with mature timber compare favorably with the commercial forests of the land.

The mangrove forests are characterized by the presence of roots that show above the surface of the ground (Figs. 235, 281, 282) and contain numerous air spaces that serve for the conduction of oxygen to the underground root system. In the genus *Rhizophora* these roots take the form of prop roots and serve both as props for the tree and for the aeration of the root system. In some cases the aerating roots are slender structures which grow vertically out of the soil, while in still other cases they have the form of knees.

Another characteristic of a large proportion of mangrove-swamp trees is the germination of the seeds while still within the fruits. This feature is most strikingly shown in the family *Rhizophoraceae*, in which the seedling bursts through the fruit and hangs down as a long, slender structure while the fruit is still attached to the tree (Fig. 385). Finally the seedling drops from the fruit, sticks in the mud, and continues to grow (Fig. 386), or it may be transported by water and deposited in a situation that is favorable to growth.

Succession and climax vegetation. The large vegetational regions, such as rain forest, deciduous forest, deserts, and arctic tundra, are determined by climate, the principal factors being moisture and temperature. In all extensive regions there are, however, minor areas in which the vegetation is the result not of the general climatic complex but of purely local conditions such as the nature of the substratum or the interference of man. Vegetation that is in a stable condition and represents the highest type that the climate can support is climax vegetation. Before vegetation reaches a climax, or stable condition, it may pass through many successive stages that are influenced by the local environment. The giving way of one type to another is known as succession.

In a region in which tall forest is the climax type there may be a lake which results in the presence of several local types of vegetation. The vegetation in the deepest part of the lake in which there are rooted plants may consist entirely of submerged plants, and between these and the forest the following types of vegetation may occur in successively shallower water: plants with floating leaves, erect monocotyledons projecting out of the water, and a growth of shrubs. The level of the water in lakes does not remain constant; on the contrary, the depth of the water tends to become less and less. This is due to the fact that material is constantly being deposited in the lake and so raises the level of the soil, while at the same time the stream leaving the lake wears down its bed and thus lowers the level of the water in the lake. As the water becomes shallower the submerged plants will invade the bare area toward the center of the lake, while the plants with floating leaves will invade the areas formerly occupied by submerged plants. Likewise the erect monocotyledonous plants will invade the areas previously occupied by the plants with floating leaves, while the forests will invade the area which was swampy as the latter becomes dry. Thus there is a series of successions between the deeply submerged bare ground and the climax forest.

Rocks may support only a growth of lichens, but as the rock weathers and soil accumulates there is a series of invasions which ends with the climax forest.

On tropical coasts, mud flats are occupied by mangrove-swamp forest, but as the land is raised this is succeeded by the forest of the dry land and finally by the climax type of the region.

The types of plant successions are very varied, are due to a great variety of local conditions, and lead to many types of climax vegetation. A study of successions shows that vegetation is not static but dynamic, and that much of it is unstable and changing. Just as an individual passes through many stages of development before reaching maturity, so plant communities go through various stages, or successions, before the climax type is produced.

CHAPTER XIII

THE FLOWER

The flowers of plants are reproductive structures whose function is the production of seed. Many flowers are very beautiful, are greatly enjoyed by man, and are used by him for purposes of ornament. From the standpoint of the plant, however, the beauty of the flower is important only in so far as it aids in the production of seed.

REPRODUCTION

Asexual reproduction. Plants have two methods of reproduction, *sexual* and *asexual*. The latter method consists simply in the separation of a portion from the parent plant and the growth of this portion into a complete plant. Many of the lower plants are reproduced asexually by a single cell. A large number of higher plants reproduce vegetatively by sending out shoots which take root and produce new plants (Fig. 5). In many cases the part of the shoot which connects the two plants dies, thus leaving them entirely separate. This method is particularly characteristic of plants with underground or prostrate stems, such as grasses that have long runners. It is also frequently seen in the aerial parts of plants, where a shoot takes root and produces a new individual. Another method of asexual reproduction is the production of bulblets. Many plants that grow from underground bulbs or corms reproduce by the multiplication of these, as is the case with the gladiolus. Bulbs may be produced on flowering shoots, as in *Agave* and the onion. Many plants produce suckers which can be removed and used to produce new plants; conspicuous examples are bananas (Fig. 91) and pineapples. A method of artificial reproduction frequently used is to cut off a portion of a stem, known as a cutting, and plant it in the ground. Under favorable conditions the cutting produces roots and leaves and grows into a new plant. In a few instances leaves of plants may fall to the ground and grow into new plants, as in *Bryophyllum* (Fig. 102) and *Begonia.* A considerable number of plants can be artificially reproduced by the use of leaf cuttings. Some ferns reproduce regularly by having the tip of a long leaf reach the ground, send out roots, and grow into a new plant (Fig. 101).

Sexual reproduction. Sexual reproduction is reproduction in which two cells unite to form a single one from which a daughter organism develops. This method of reproduction is characteristic of the vast majority of plants. Among the higher plants the flower is the organ for sexual reproduction.

THE STRUCTURE OF THE FLOWER

Parts of the Flower. In a complete flower, that is, one which has all the parts of a typical flower, there are four kinds of structures besides the stalk (Figs. 283, 284). There are one or more *pistils*, *stamens*, a *calyx*, and a *corolla.* The pistils and stamens are the essential parts; the others are accessory.

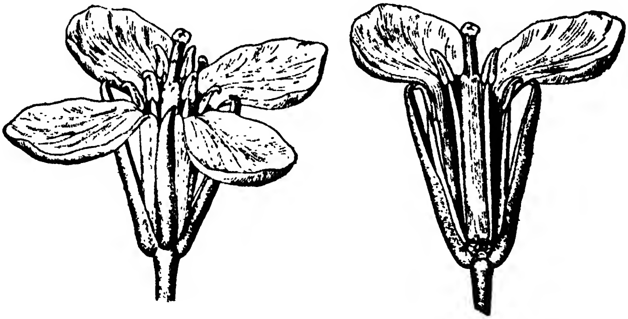


Fig. 283. Flower of kale (a variety of cabbage, *Brassica oleracea*)

To the left is a whole flower, showing the sepals below, the large petals next, within them the long stamens, and in the center the pistil, composed of an ovary surmounted by the style, which terminates in the stigma. To the right is a flower from which one sepal, two petals, and two stamens have been removed

Some flowers are *regular*, — that is, all the members of each set of organs are alike (Figs. 284, 295–297), — while others are *irregular* (Figs. 285, 286).

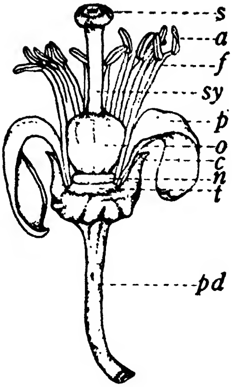


Fig. 284. Flower of grapefruit (*Citrus*) with a portion of calyx and some of petals and stamens removed

pd, pedicel; *t*, torus; *n*, nectary; *c*, calyx; *p*, petal; *f*, filament of stamen; *a*, anther; *o*, ovary; *sy*, style; *s*, stigma. (× 1)

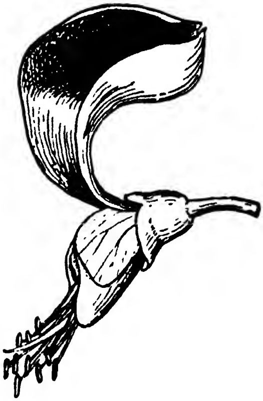


Fig. 285. Irregular flower of a legume, *Erythrina fusca* (× ⅓)

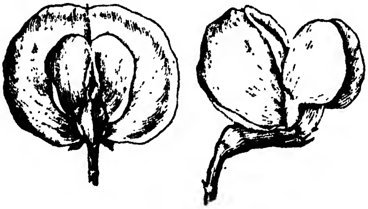


Fig. 286. Irregular flower of a garden pea

Left, front view; right, side view. The stamens and pistil are largely hidden by the petals

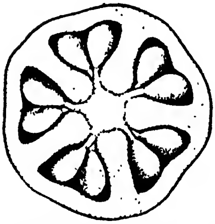


Fig. 287. Cross section of an ovary of *Hibiscus*, showing five cavities or cells containing ovules. (× 10)

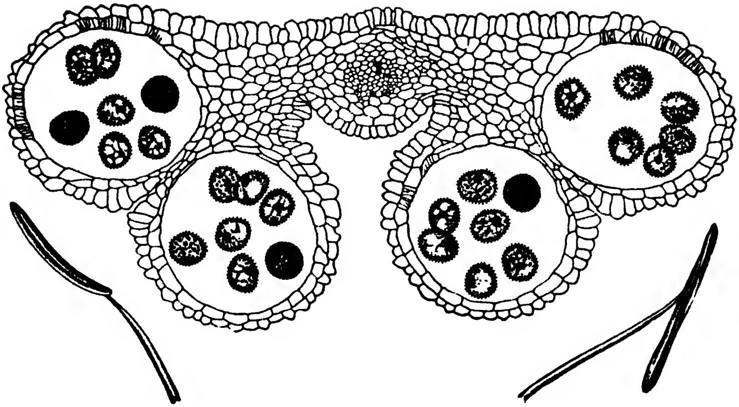


FIG. 288. Cross section of anther, with pollen grains in pollen sacs (× 85). At sides, two types of stamens

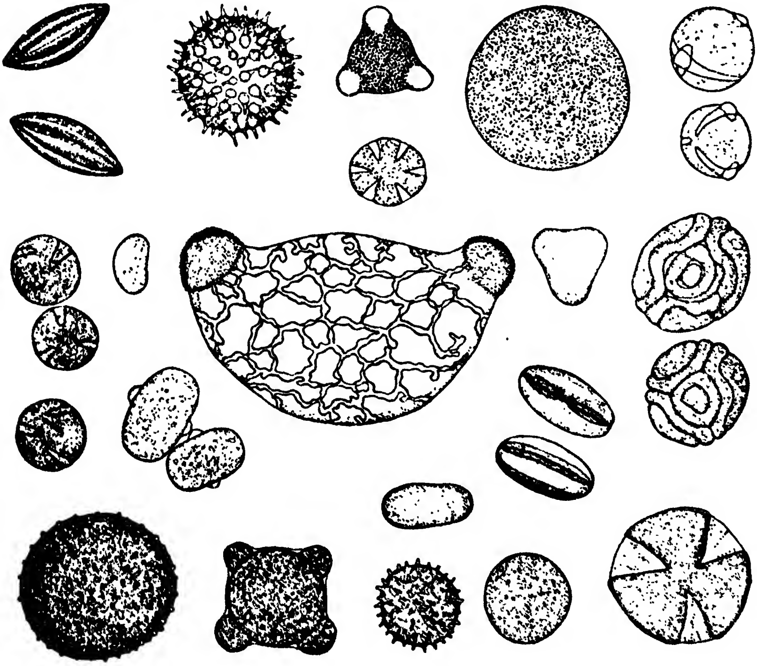


FIG. 289. Pollen grains of various plants. (× 225)

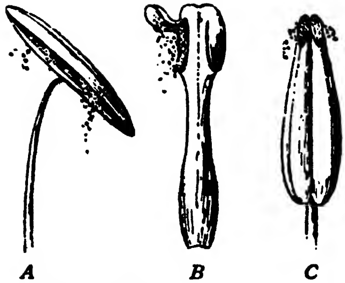


FIG. 290. Modes of discharging pollen

A, by longitudinal slits in the anther cells (*Amaryllis*); *B*, by uplifting valves (barberry); *C*, by a pore at the top of each anther lobe (nightshade). After Baillon

Pistils. The pistils are usually found in the center of the flower (Fig. 284). A pistil consists of an enlarged basal portion called the *ovary*, a terminal part known as the *stigma*, and, usually, a long, slender structure, the *style*, which connects the ovary with the stigma. The ovary contains one or more cavities (Fig. 287) within which are found small oval or egg-shaped *ovules*. An ovule is attached to the ovary wall by a small stalk called the *funiculus*. Each ovule contains an *egg*, which is the female reproductive cell.

Stamens. A stamen consists of two parts (Fig. 288): a large terminal portion, which is the *anther*, and a stalk known as the *filament*. The anther contains cavities called *pollen sacs*, in which *pollen grains* are produced (Figs. 288, 289). Pollen grains from the anthers are carried by the wind, by insects, or by other agencies

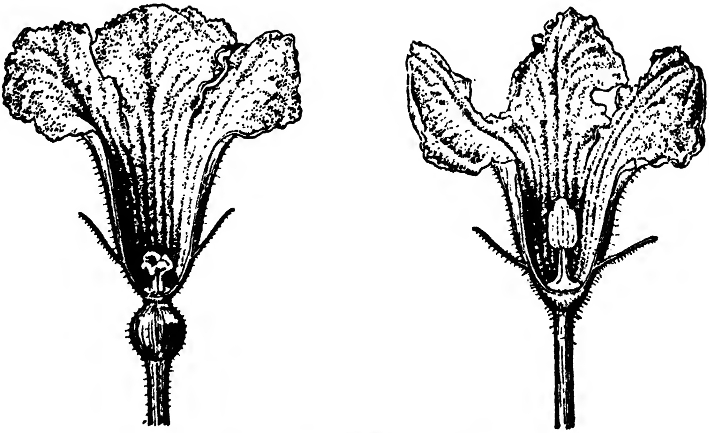


FIG. 291. Flowers of pumpkin

Left, female flower with calyx and corolla attached above rounded ovary; right, male flower. (× ½) and deposited on the stigma of the pistil. This transfer is known as *pollination,* and when it has taken place the flower is said to be *pollinated.* The method by which the anthers open to discharge the pollen varies in different cases. Three methods are shown in Fig. 290.

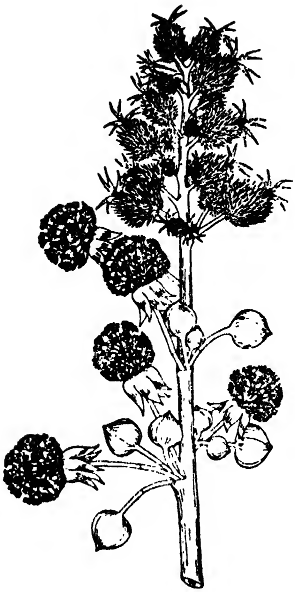


FIG. 292. Flowers of castor-oil plant

Above, female flowers; below, male flowers. (× 1)

Fertilization. A pollen grain, after being deposited on the stigma, produces a long tube which grows down through the stigma and the style and enters one of the ovules in the ovary (Fig. 4). Two male nuclei are found at the end of this tube. One of these enters the egg of an ovule and fuses with the nucleus of the egg. This fusion of male and female nuclei is called *fertilization,* and the flower is said to be *fertilized* when this has taken place. After fertilization the ovule develops into a seed, while the whole ovary becomes a fruit.

Sexuality of flowers. Usually stamens and pistils are found in the same flower (*bisexual flowers*) (Figs. 283, 284), but frequently

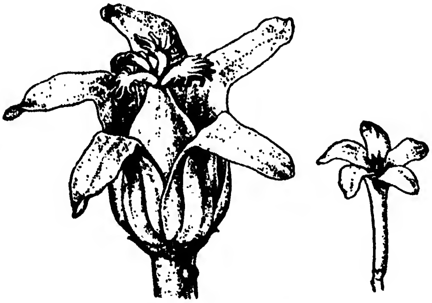


FIG. 293. Flowers of papaya (*Carica papaya*)

Left, female; right, male. (× ⅓)

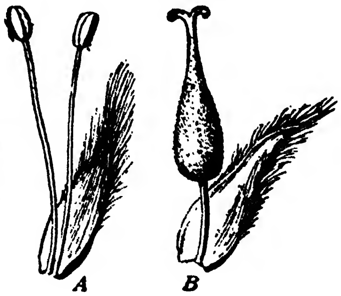


FIG. 294. Flowers of willow

A, male flower; *B*, female flower. (Magnified.) After Decaisne

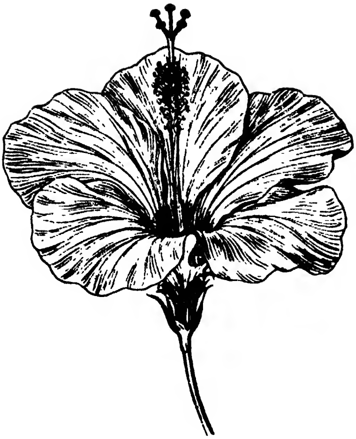


Fig. 295. Flower of ***Hibiscus***

The filaments of the stamens are united to form a tube which surrounds the style. (× $\frac{2}{5}$)

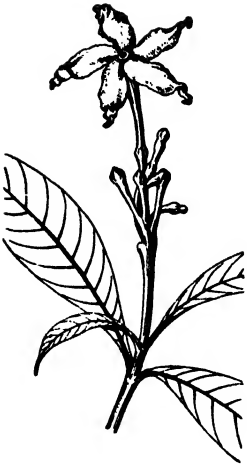


Fig. 296. Flower of ***Tabernaemontana pandacaqui***

The corolla is composed of a long tube with five prominent lobes. (× $\frac{2}{5}$)

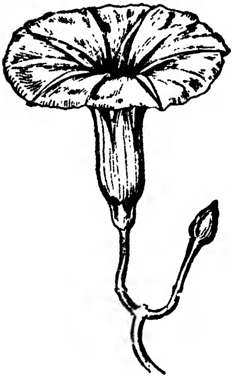


Fig. 297. Flower with a bell-shaped corolla. (× $\frac{1}{2}$)

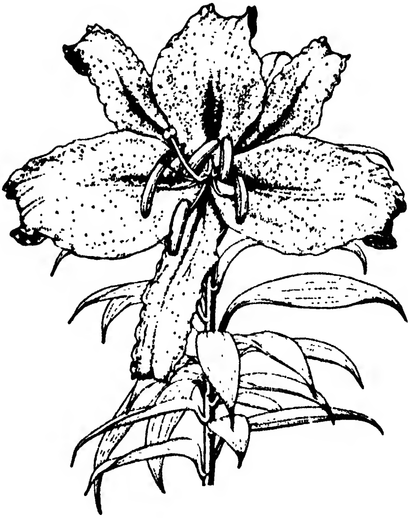


Fig. 298. Flower of lily, showing similarity of petals and sepals

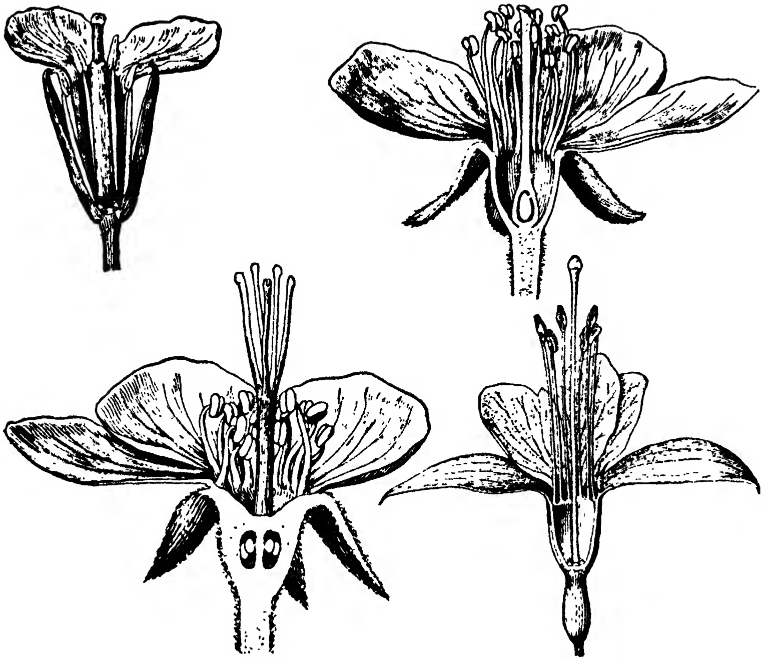


Fig. 299. Upper left, hypogynous flower of kale. Upper right, perigynous flower of plum. Lower left, epigynous flower of apple. Lower right, epigynous flower of *Fuchsia*

they occur in different ones (*unisexual flowers*). When they occur in different flowers, both kinds of flowers may be on the same plant (*monoecious* plants) (Figs. 291, 292), as in the cases of corn and the castor-oil plant, or they may be on different plants (*dioecious* plants) (Figs. 293, 311).

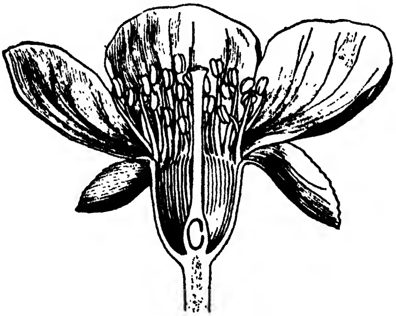


Fig. 300. Section of flower of cherry with simple pistil consisting of a single carpel

Perianth. While the stamens and pistils are the essential parts of a flower, they are usually surrounded by thin, expanded structures which collectively constitute the *perianth.* In a complete flower the perianth is divided into an interior part, or *corolla,* and an outer part, or *calyx* (Figs. 283, 284). In some flowers there is no perianth (Figs. 294, 312).

Corolla. The corolla may be composed of a number of separate thin units, the *petals* (Fig. 295), usually white or bright-colored, or of a more or less tubular (Fig. 296), bell-shaped, or funnel-shaped structure (Fig. 297) with lobes which represent the petals. It seems that the function of the conspicuous, bright-colored corolla is to attract the insects, or sometimes small birds, that carry pollen from one flower to another. Bright-colored or conspicuous flowers are usually pollinated by insects.

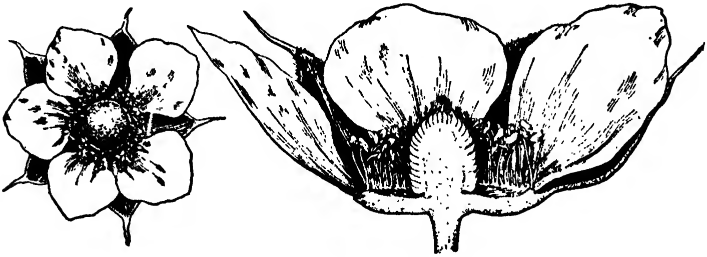


FIG. 301. Flower of raspberry

Left, top view showing numerous pistils surrounded by numerous stamens, these by five petals, and these in turn by five sepals. Right, longitudinal section showing numerous simple pistils growing on a projection from the torus

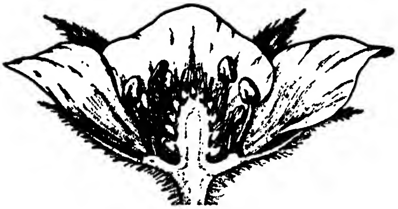


FIG. 302. Section of a strawberry flower

There are numerous simple pistils on the projection of the torus. Around these are the stamens, then the petals and sepals

Calyx. The calyx, like the corolla, may be composed of a number of separate units, which in this case are called *sepals* (Fig. 283), or of a somewhat tubular or funnel-shaped structure with lobes which represent the sepals. The calyx is typically small and green. The function of the calyx seems to be to protect the inner parts of the flower before the flower bud has opened.

Frequently the perianth consists of only one set of structures, and in such a case this set is regarded as a calyx, the corolla being considered as absent. When there is no corolla, the calyx is often bright-colored and conspicuous and takes the place of the corolla in its function of attracting insects. In many of the monocotyledonous plants the sepals are large, bright-colored, and very similar in appearance to the petals (Fig. 298).

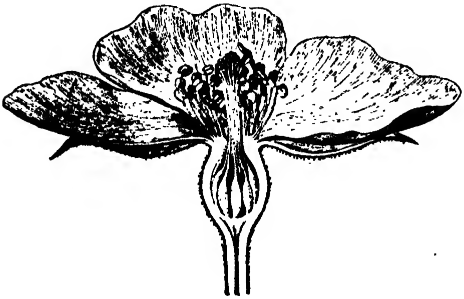


Fig. 303. Section of a rose flower showing numerous separate pistils located in urn-shaped torus

Flower stalk. The flowers are joined to the stem by a central axis, or stalk, which is usually composed of two parts: the stalk proper, which is known as the *pedicel*, and an expanded terminal portion, the *torus*, or *receptacle*, on which the other parts of the flowers are borne (Fig. 3).

Arrangement of floral parts. When the torus is convex and the other floral parts are attached below the ovary, the flower is said to be *hypogynous* (Figs. 284, 299). In some cases the torus forms a cup-shaped structure at the summit of which are borne the sepals, petals, and stamens. Such flowers are *perigynous* (Fig. 299). When the torus is not merely a cup-shaped structure surrounding the ovary but is fused to the ovary so that the sepals, petals, and stamens appear to be attached above the ovary, the flower is said to be *epigynous* (Figs. 291, 299).

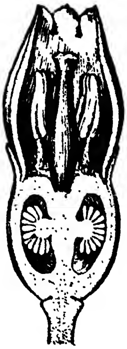


Fig. 304. Section of flower of *Vaccinium* showing compound ovary with a single style

Simple and compound ovaries. A carpel is a simple pistil with one cavity and one style (Fig. 300). Often several carpels are united to form a compound ovary (Fig. 287). In a flower there may be a single ovary consisting of a single carpel, as in the cherry (Fig. 300), peach, or plum (Fig. 299).

In the raspberry (Fig. 301) and strawberry (Fig. 302) a number of separate carpels are located on a central projection of a torus. In the rose there are a number of separate carpels which are located within an urn-shaped torus (Fig. 303). Compound ovaries composed of two or more united carpels are very common (Fig. 287), as in cucumber, squash, melons, tomato, etc. In compound pistils the stigmas may be separate (Fig. 295) or united to form a single pistil (Fig. 304).

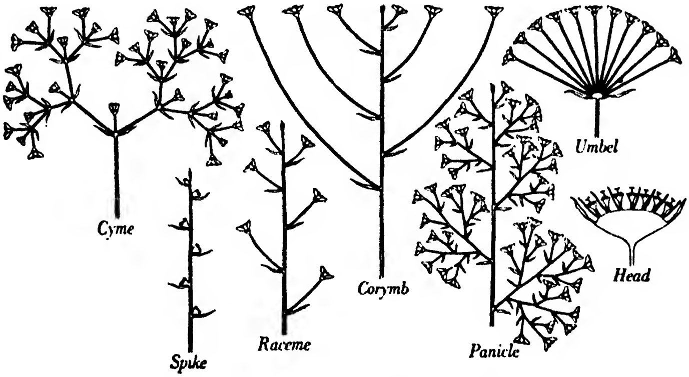


FIG. 305. Diagrams of some inflorescences

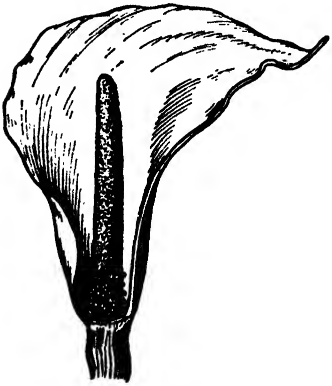


FIG. 306. Section of flower of calla lily showing spadix with female flowers below and male flowers above

Inflorescences. Flowers are borne in different ways on different plants, and various types of inflorescences are given distinctive names.

Cyme. When a flower terminates a stem and the subsequent development of the inflorescence is due to auxiliary branches, the inflorescence is a cyme (Fig. 305).

Spike. When sessile flowers (that is, flowers without stalks) are borne on the side of a simple undivided axis, the inflorescence is a spike, as in plantain.

Catkin. A unisexual scaly spike which falls off in one piece after flowering or fruiting is a catkin, as in birch, poplar, and willow.

Spadix. A spadix is a fleshy spike more or less enclosed by a large modified leaf known as a spathe, and is characteristic of the aroids, such as the calla lily and taro (Figs. 306, 318).

Raceme. A raceme is similar to a spike except that the flowers are stalked. This is a very common type of inflorescence.

Corymb. A corymb is similar to a raceme except that the lower flowers have longer stalks than the upper ones so that the inflorescence is more or less flat-topped.

Panicle. A panicle is an open, branched racemose inflorescence (Fig. 305). It is a very common type of inflorescence, found in many grasses.

Umbel. When the flowers all appear to arise from the same place and have stalks of equal length, the inflorescence is an umbel, as in carrot and celery.

Head. A head is a globular or somewhat flattened cluster of sessile flowers (Figs. 305, 307).

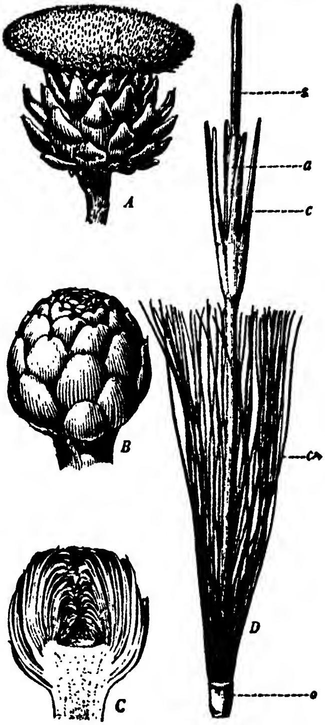


Fig. 307. **Flower head of artichoke (*Cynara scolymus*)**

The artichoke belongs to the sunflower family. *A*, head; *D*, a single flower; *s*, stigma; *a*, anther; *c*, corolla; *ca*, calyx; *o*, ovary. *B*, flower head in bud, the edible stage. *C*, section of bud. Note that it is the young flower head and a portion of the bracts that are edible

POLLINATION

Cross-pollination. Most flowers are so arranged as to facilitate the transfer of pollen from the stamens of one flower to the stigma of another (*cross-pollination*) rather than from the stamens to the stigma of the same flower (*self-pollination*). When the stamens and pistils occur in different flowers, the flowers must be cross-pollinated. Cross-pollination is also usual in bisexual flowers. One of the simplest arrangements which assures this is the maturing of the stigmas and anthers at different times (Figs. 308, 309). Another method is seen in the primrose, where on some plants all flowers have the stigma above the anthers and on other plants the anthers are above the stigmas. A bee entering either type of flower would have the pollen dusted on him in such a way that he would leave it on the stigma of the opposite type of flower.

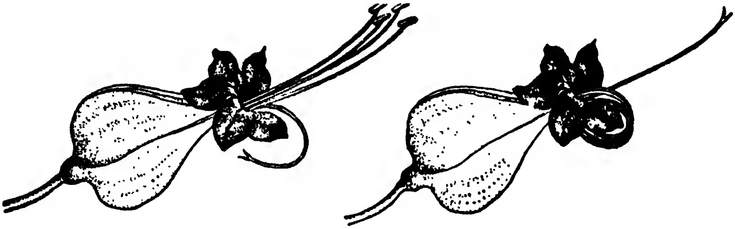


FIG. 308. Flowers of *Clerodendron*

Left, presentation of stamens; right, presentation of stigma, the stamens having coiled under the petals. (× 1)

The most usual agents for the transfer of pollen from one plant to another are insects and wind. Other agencies, such as small birds, may be effective. In submerged plants the transfer may be made by water.

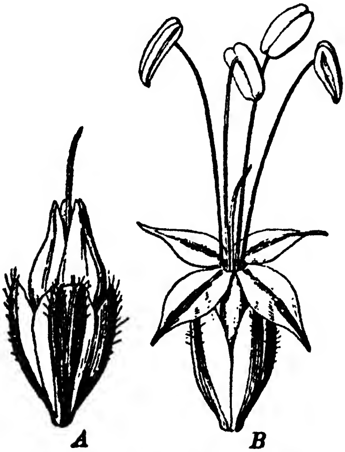


FIG. 309. Flowers of plantain (*Plantago lanceolata*)

A, earlier stage, pistil mature, stamens not yet appearing outside the corolla; *B*, later stage, pistil withered, stamens mature. Six times natural size

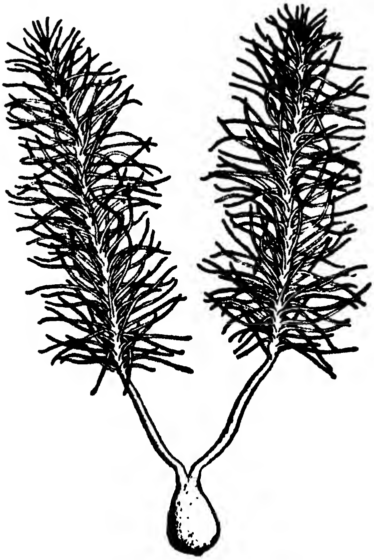


FIG. 310. Feathery stigmas of a grass. (× 12)

Wind pollination. Some flowers have no perianth at all, and others have very inconspicuous ones. In such cases the pollen is frequently produced in large quantities and is carried by the wind from one flower to another. Indian corn is a good example of a plant that has rather inconspicuous flowers and is wind-pollinated. The male flowers occur at the top of the plant in what is commonly known as the tassel. The female flowers are produced lower down in heads, which after fertilization become the ears of corn. The long, silky hairs which project from these ears are the styles and stigmas. The female flowers are thus in a favorable position to have pollen blown to them from the male flowers of other plants.

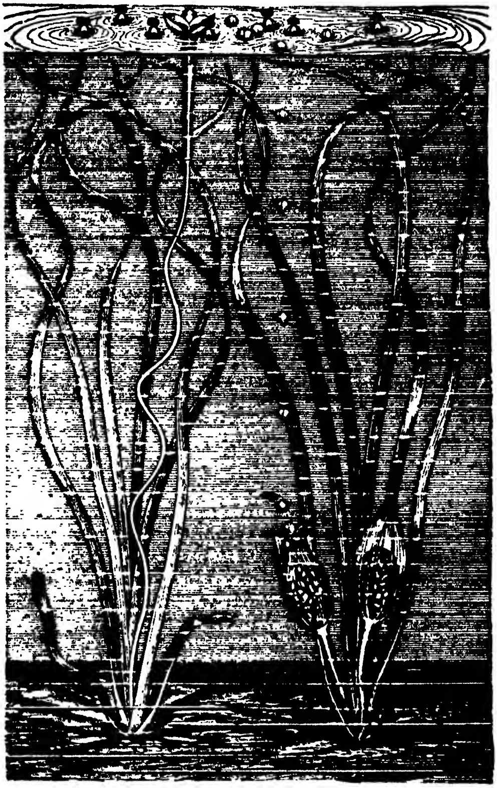


FIG. 311. Pollination of *Vallisneria gigantea*; size of flowers exaggerated

Left, a female plant with a flower floating on the surface of the water; right, a male plant with two spikes of male flowers. The covering of the spike at the left is open and the flowers are becoming detached and rising to the surface, where they open and float. The stamens of one male flower are in contact with the stigma of the female flower

Grasses, many trees, and some shrubs and herbs are pollinated by the wind. To insure pollination, wind-pollinated species produce large quantities of pollen; and when the pistils and stamens occur in separate flowers, the male flowers are very much more numerous than the female ones. The production of large quantities of pollen is evidently necessary when most of it must be wasted, as is the case with wind-pollinated species, where it is only by rare chance that a grain of pollen will be blown to the stigma of the same species. The stigmas of wind-pollinated plants are usually broad and feathery, and so afford a large surface for catching pollen (Fig. 310). This naturally increases the chance that pollen will reach the stigma. Many wind-pollinated species produce their flowers above the foliage, as is usually true of grasses, or at a time when they do not have leaves, as is the case with numerous trees of the temperate zone which produce their flowers early in the spring before the leaves have appeared. Either of these arrangements increases the chance of pollen's reaching the stigma.

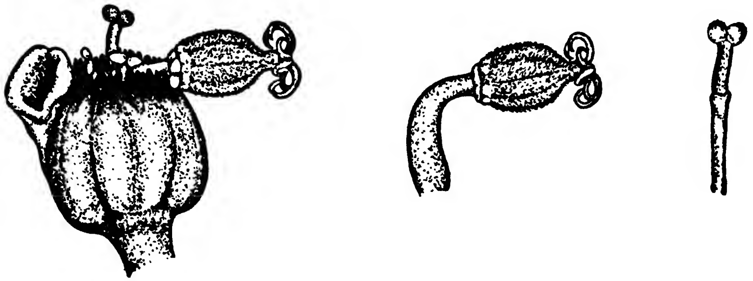


FIG. 312. Flowers of poinsettia (*Euphorbia pulcherrima*)

Left, flower head — at the left of the head is a cup-shaped nectary, and projecting from the head are three male flowers and one female flower; center, a single female flower composed of a stalk and pistil; right, a single male flower composed of a stalk and a single stamen. Compare with Fig. 98. (× 2½)

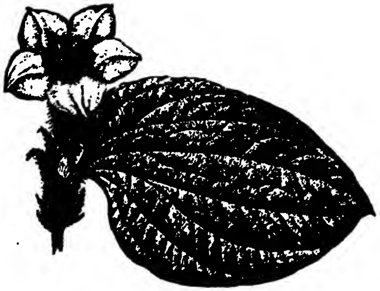


FIG. 313. *Musaenda erythrophylla*

The most conspicuous part of this flower is a single greatly-enlarged red calyx-lobe

Wind-pollination is especially adapted to species which grow together in large numbers, rather than to those which are scattered in mixed stands. Since grasses often cover quite extensive areas, they are very well adapted to this method of pollination, as are also forest trees which grow in stands of one or a few species. Wind pollination is much more frequent in the forests of the temperate zone, which are composed of one or a few species, than in the forests of the moist tropics, where as a rule the stand is made up of a great variety of trees.

Insect pollination. Insects are attracted to flowers by their odor, by their conspicuousness, or by both odor and conspicuousness, and visit them for the purpose of collecting nectar and pollen, which serve them as food. While visiting a flower the body of an insect becomes dusted with pollen, which may subsequently be caught on the stigma of another flower visited.

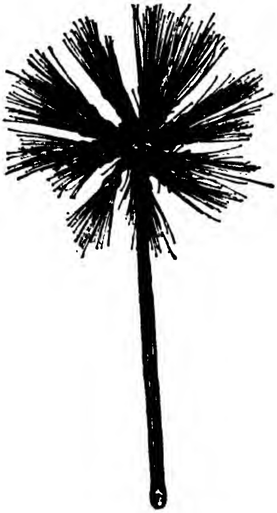


FIG. 314. Flower cluster of a legume, rain tree (*Enterolobium saman*), showing brightly colored stamens. (× ⅓)

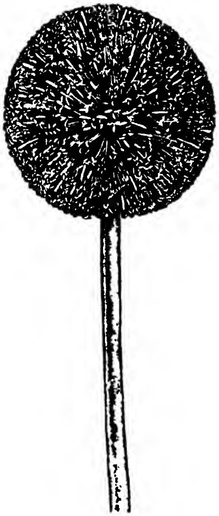


FIG. 315. Showy flower head of a legume, *Leucaena glauca*

The conspicuousness of the head is due to white stamens and pistils. (× 1)

Nectar is a sweet liquid that is secreted by glands which may be on the torus (Figs. 284, 312) or on the petals, or elsewhere. Conspicuous cavities in the petals frequently contain nectar glands. Bees use nectar in making honey.

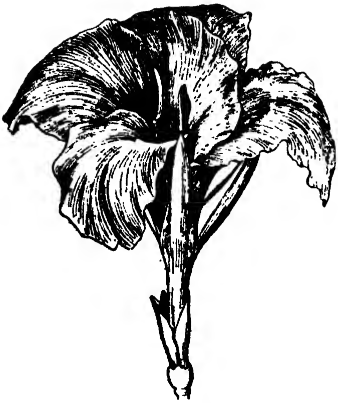


Fig. 316. Flower of *Canna*

Below is the ovary surmounted by three small sepals, within which are three narrow petals. The conspicuous parts are the stamens, the central one of which bears an anther on the margin to the left. In the center of the flower is the stigma. (× ⅖)

Many flowers that do not secrete nectar produce large quantities of pollen, which serves as food for insects. Although the insects may use a considerable part of the pollen, nevertheless some of it sticks to their bodies and is carried to the stigmas of other flowers.

Insect-pollinated species frequently have pollen which either is sticky or is furnished with numerous projections which help make the pollen adhere to the body of an insect, while the bodies of the pollinating insects are usually hairy. When the stigma of a flower is mature, it has a sticky surface to which pollen grains adhere when the stigma is touched by a part of an insect on which pollen has been caught.

Water pollination. A few species of submerged water plants have female flowers that lie on the surface of the water and male flowers that become detached, float to the female flowers, and deposit pollen on the stigmas. A well-known example is the common eel grass, *Vallisneria* (Fig. 311).

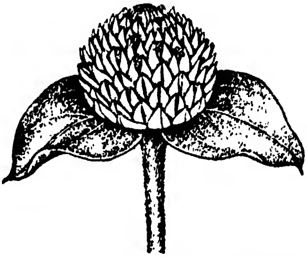


Fig. 317. Flower head of bachelor's button (*Gomphrena globosa*)

The flowers are small, and each is surrounded by two conspicuous white or brightly colored specialized leaves or bracts. (× 1)

Conspicuous flowers. In typical flowers the conspicuous part is the perianth, but in many insect-pollinated species the perianth is lacking or inconspicuous, while other structures are showy and serve for the attraction of insects (Figs. 98, 312, 313).

In *Acacia* and many others of the bean family the perianth is inconspicuous, but a large number of flowers with long stamens are crowded together into a showy feathery ball (Figs. 314, 315).

In *Canna* the calyx and corolla are rather inconspicuous, and the bright-colored part of the flower is composed of petal-like stamens (Fig. 316).

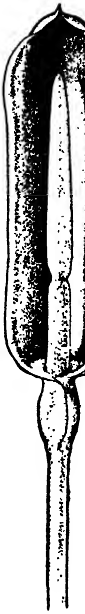


Fig. 318. Flower cluster of elephant's-ear (*Alocasia indica*)

The inflorescence is in the center, the upper part being sterile and the lower bearing numerous flowers; the whole is surrounded by a specialized leaf called a spathe. (× ¼)

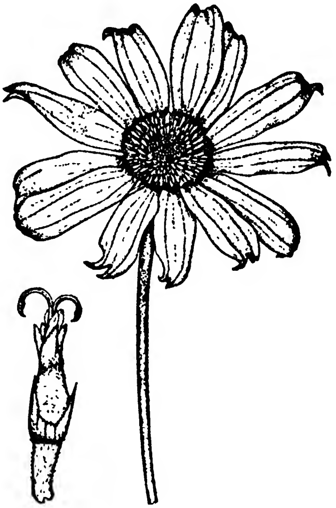


Fig. 319. Single flower (× 1⅔) and flower head (× ⅓) of a sunflower (*Helianthus cucumerifolius*)

In the single flower the parts from below upward are ovary, calyx, corolla, stamens, and stigma

In many species the flowers themselves are small and inconspicuous, but they are surrounded by large, brightly colored leaf-like bracts (Figs. 100, 317). In the family *Araceae* a large number of small flowers are crowded together on a long stalk, and the whole flower shoot is more or less surrounded by a large white or bright-colored bract called a spathe (Figs. 306, 318).

In many cases individual flowers are not showy themselves, but they are crowded together in groups which are very conspicuous. In the family *Compositae* this condition is carried so far that the individual flowers are crowded into heads which superficially resemble single flowers (Figs. 307, 319, 320), as is the case with the sunflower, cosmos, daisy, and chrysanthemum.

Odors of flowers. Many flowers possess odors which serve to attract insects, and a large number of inconspicuous flowers are pollinated by insects that are attracted by the odor. Conspicuous flowers frequently have odors, although in many cases they are odorless. The odors are due to *essential oils* which are volatile and odoriferous.

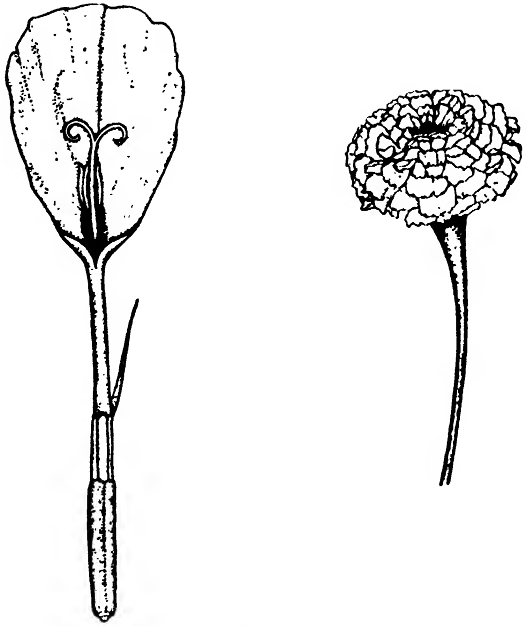


Fig. 320. Single flower (× 2) and flower head (× ½) of marigold

In the single flower the expanded portion is the corolla; in the center of this are shown the style and the stigma surrounded by stamens

The essential oils of flowers are extensively employed in the manufacture of perfumes, toilet waters, and face and sachet powders. Various methods such as steam distillation, extraction with fats (preparation of flower pomades), and extraction with volatile solvents are used to obtain the perfume oils from flowers.

FERTILIZATION

Growth of pollen tube. The transfer of the pollen from the anthers to the stigma is known as pollination, and is followed by the growth of the pollen tube, which leads to fertilization. After the pollen grain has been deposited on the stigma (Fig. 321), it sends out a protuberance, or *pollen tube* (Figs. 322, 323), which grows down through the style till it reaches the ovule. In passing through the style the tube absorbs nourishment from the cells of the style. After reaching the ovary the pollen tube, continuing to grow, enters an ovule (Fig. 4).

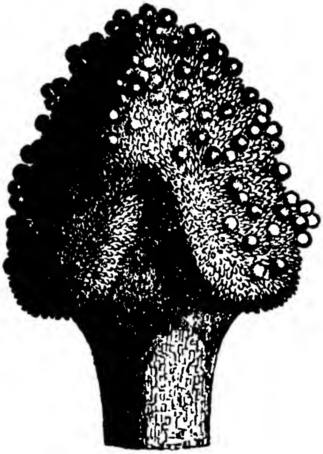


Fig. 321. Pollen grains deposited on a stigma

After Baillon

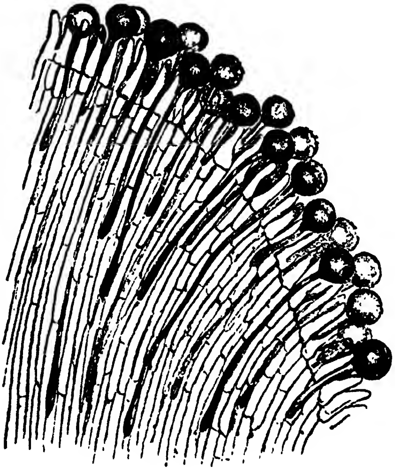


Fig. 322. Pollen tubes growing on a stigma

After Baillon

There are three nuclei in the pollen tube. One of these is known as the tube nucleus, and appears to govern the activity of the pollen tube; the other two are male nuclei. Their functions will be better understood after we have considered the ovule.

Structure of ovule. The ovule (Fig. 324) consists of a central mass, the ***nucellus***, which is joined to the ovary wall by a stalk, the ***funiculus***, and is surrounded by two cellular membranes, the ***integuments***. The ovule may be straight (Fig. 326), but more usually it is bent back on the funiculus, with the outer integument fused to the funiculus, as shown in Fig. 324. The end of the nucellus that is attached to the funiculus is known as the *chalazal* end. At the opposite end of the ovule there is an opening, the *micropyle*, which extends through the integuments, and through which the pollen tube passes when it enters the ovule. In the nucellus at the mi-

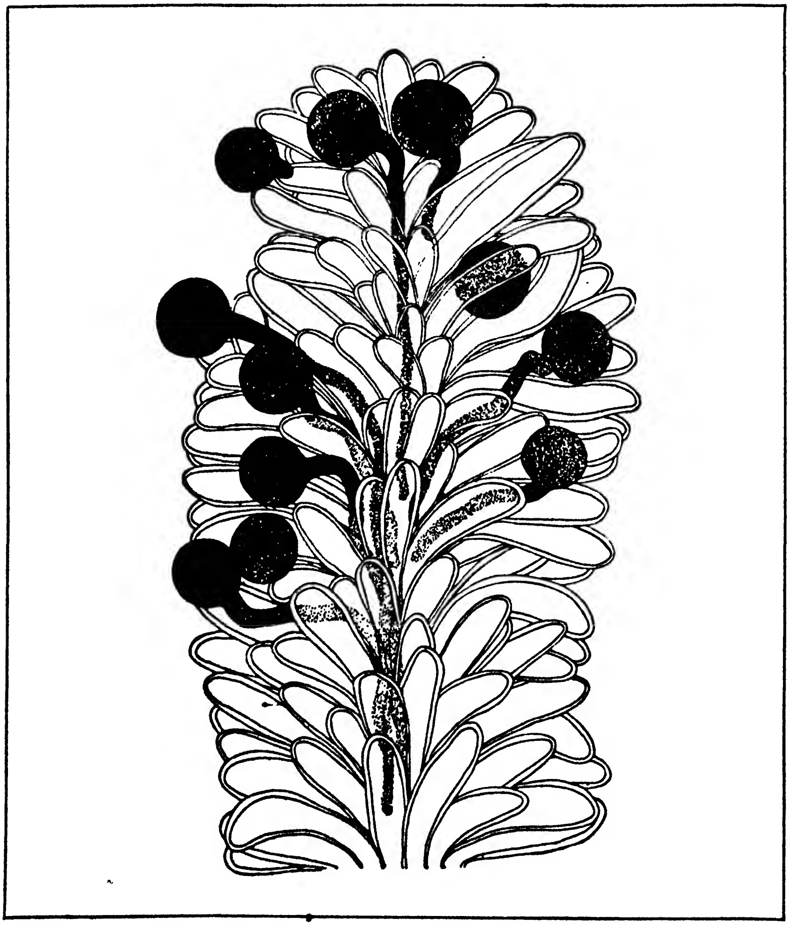


Fig. 323. Germination and growth of pollen grains on a stigma of the purslane (*Portulaca oleracea*). (× 165)

cropylar end is the *embryo sac*, which is usually somewhat oval. Within this embryo sac are six cells and two free nuclei, the *polar nuclei*. The cells occur in a group of three at the micropylar end and another group of three at the chalazal end. The three at the micropylar end consist of a large cell, the *egg*, and two small cells, the *synergids*. At the chalazal end of the sac the three cells are usually small and are known as *antipodals*. The two polar nuclei originate one at each end of the embryo sac, but later move to the center.

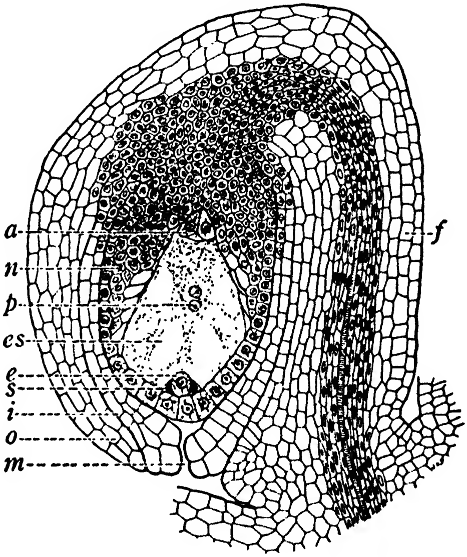


FIG. 324. Ovule of *Zephyranthes rosea*

f, funiculus; *m*, micropyle; *o*, outer integument; *i*, inner integument; *n*, nucellus; *es*, embryo sac; *s*, synergid; *e*, egg; *p*, polar nucleus; *a*, antipodal cell. (× 115)

Development of ovule. The ovule starts as a small conical projection. Soon the inner integument appears as a collar around the young ovule and grows upward (Fig. 325). It is followed by a second integument which grows over it. The two integuments

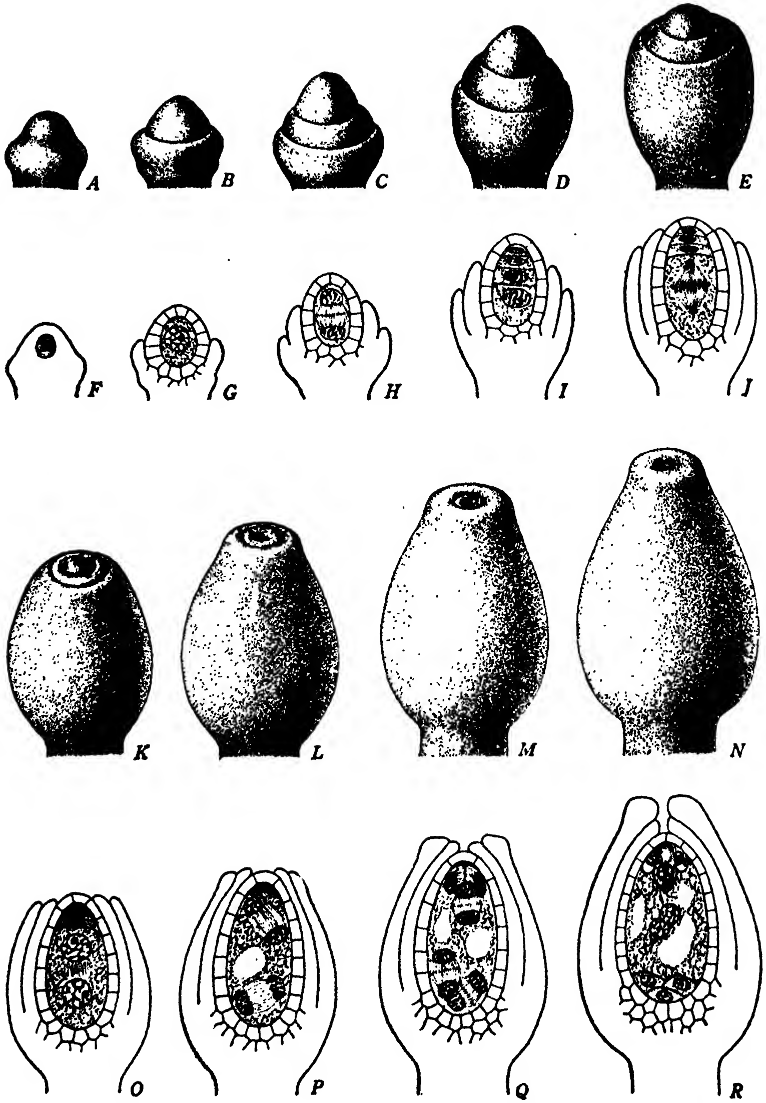


Fig. 325. Diagrammatic representation of development of ovule

A–E, *K–N*, growth of integuments; *F*, *G*, gynospore (megaspore) mother cell; *H*, *I*, two divisions of nucleus to form four spores; *J*, three spores compressed, one enlarged, its nucleus dividing; *O*, binucleate stage of embryo sac, upper spores degenerating; *P*, four-nucleate stage; *Q*, eight-nucleate stage; *R*, cells formed (above, egg, synergids; below, antipodal cells; center, polar nuclei) continue to grow until they have covered the nucellus (Fig. 325).

At an early stage, a large cell known as a spore mother cell is differentiated in the nucellus. This continues to grow, and forms a row of four cells known as spores. The three nearest the apex degenerate, while the lowest enlarges and gives rise to the embryo sac (Fig. 325). The nucellus divides to form two nuclei. Each of these then divides to form two nuclei, which results in a four-nucleate stage. Up to this time there are no walls in the embryo sac. The four nuclei divide to form eight. Walls are then formed in such a way that there are three cells, an egg and two synergids, at the micropylar end, while at the chalazal end there are three antipodals (Figs. 324, 325, 326). The nuclei which are left free in the embryo sac are the polar nuclei.

Development of pollen tube. When the pollen grain is first formed it contains one nucleus. This nucleus gives rise to three nuclei, usually before but sometimes

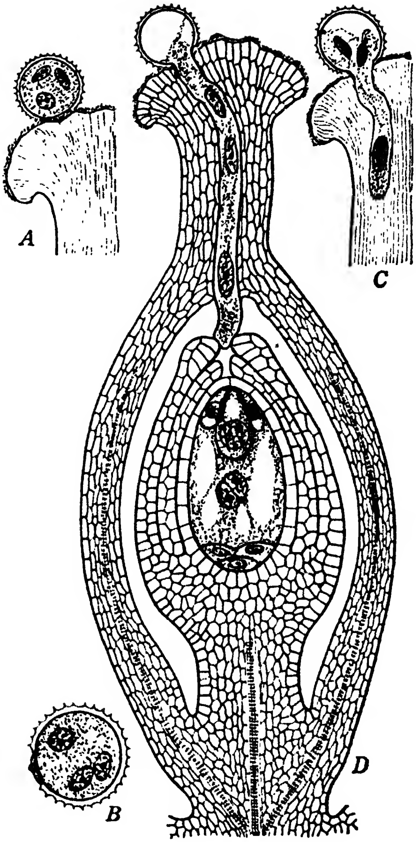


Fig. 326. Diagrammatic representation of an ovary with a straight ovule and also of the development of the pollen tube

B, a pollen grain with a tube nucleus and two male nuclei; *A*, pollen grain on stigma; *C*, pollen tube growing into stigma; *D*, the pollen tube entering the micropyle. The large cell in the micropylar end of the embryo sac is the egg, while the two at the sides of the egg are the synergids. At the other end of the sac are three antipodal cells. In the center the two polar nuclei are fusing after the germination of the pollen grain. These nuclei consist of a tube nucleus and two male nuclei (Fig. 326). The tube nucleus apparently has to do with the growth of the pollen tube, as it enters the tube at an early stage and during the growth of the tube towards the ovule it precedes the two male nuclei. The pollen tube grows down through the style and toward the ovule, which it enters by way of the micropyle.

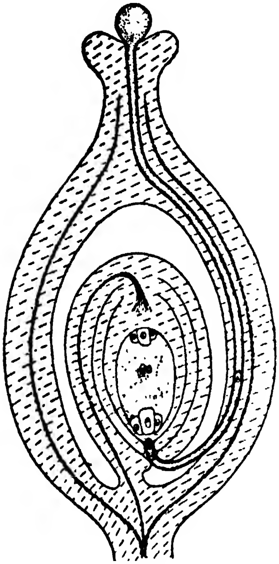


FIG. 327. Diagram of section of an ovary with an ovule bent back on the funiculus. Note growth of pollen tube toward embryo sac

Within the ovary is a single ovule; in the center of the ovule is the embryo sac surrounded by the nucellus and this by two integuments. A pollen tube has grown from the pollen grain on the stigma and has entered the ovule through the micropyle

Fertilization. When the pollen tube reaches the ovule, it grows through the micropyle (Figs. 327, 328) and then into the embryo sac, where it discharges the two male nuclei. One of these enters the egg and fuses with the nucleus of the egg (Fig. 328). This process is known as fertilization, and the product as the fertilized egg. The fertilized egg develops into an embryo, which is found in the seed, and the embryo in turn, after the germination of the seed, grows into a mature plant.

Endosperm. The male nucleus which does not fertilize the egg moves to the center of the embryo sac and fuses with the two polar nuclei to form a single nucleus known as the *endosperm nucleus*. This endosperm nucleus rapidly undergoes successive divisions to produce an *endosperm*. At first no walls are formed, and the nuclei lie freely in the cytoplasm of the enlarged embryo sac. Later walls appear, and the endosperm becomes cellular with each cell containing a single nucleus. The endosperm absorbs nourishment from the surrounding tissue and passes it on to the embryo. The endosperm may be entirely absorbed by the developing em-

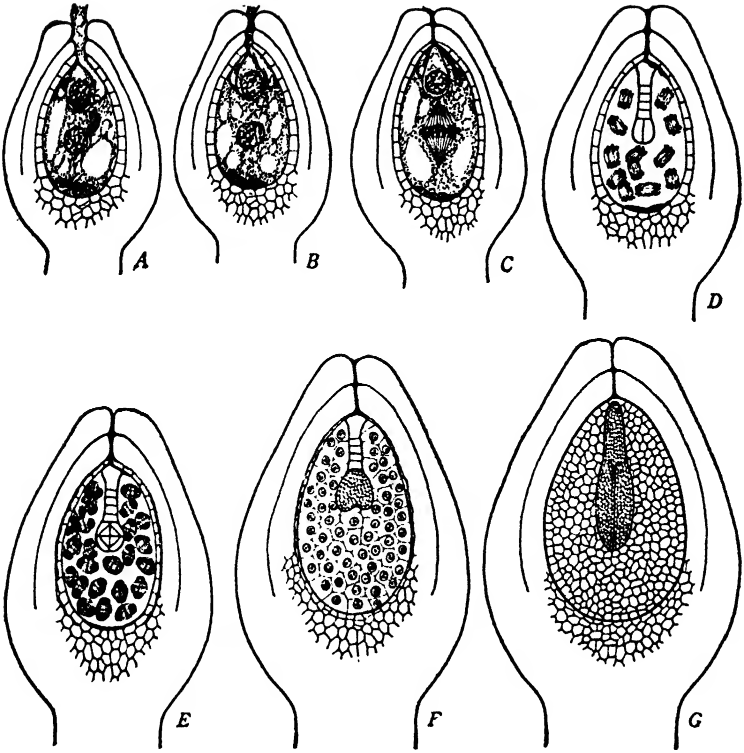


FIG. 328. Diagrammatic representation of fertilization and development of embryo

A, the pollen tube is shown as having entered through the micropyle, while a curved male nucleus lies in the egg just below the egg nucleus; the two polar nuclei have fused to form a single nucleus and the second male nucleus is near this fusion nucleus. *B*, the male and egg nuclei are nearly fused, while the second male nucleus is fusing with the nucleus formed by the fusion of the polar nuclei, to form the endosperm nucleus. *C*, the endosperm nucleus is dividing. *D*, a young embryo has developed from the fertilized egg and numerous endosperm nuclei are dividing. *E*, a more advanced stage. *F*, the cotyledons are beginning to appear on the embryo, while the endosperm has become cellular. *G*, a seed in which the embryo is surrounded by endosperm and this by two integuments

bryo before the seed becomes mature, or it may remain in the seed, surround the embryo in the mature seed, and be absorbed only during the germination of the seed (Fig. 360).

CHAPTER XIV

THE FRUIT AND THE SEED

THE FRUIT

The term *fruit*, in the botanical sense, is used to denote that part of the plant in which the seeds are found. It consists essentially of the ripe ovary, but it may also include other floral parts which are connected with the ovary. The name *fruit*, used in this sense, includes much more than the popular term *fruit*; it embraces not only what are generally known as fruits but also some vegetables, and even dry, inedible structures. To the botanist cucumbers, tomatoes, or bean pods with the included seeds are just as truly fruits as are apples and oranges.

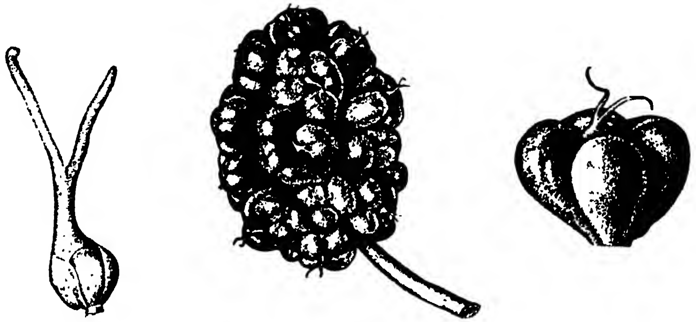


Fig. 329. Collective fruit of mulberry

Left, a female flower (× 4½); center, entire fruit (× 1½); right, single mature fruit in which the fleshy portion consists of enlarged calyx (× 3)

Collective and aggregate fruits. Most fruits are structures derived from one ovary in one flower. The wall of the ovary develops into the covering of the fruit, known as the *pericarp*, which encloses a seed. A pericarp is composed of three layers; an external *exocarp*, a middle *mesocarp*, and an internal *endocarp*. These may be so distinct that the exocarp forms a skin, the mesocarp a fleshy portion, and the endocarp a hard shell around the seed (Figs. 354, 356).

In some cases a number of separate flowers may form a *collective* fruit (Figs. 329, 330, 345), as in the pineapple (Fig. 330) and breadfruit (Fig. 331). In both of these cases the fruit is formed from a compact inflorescence in which many individual flowers are joined together from the time that they are first formed. Moreover, the inflorescence, except for size, has an appearance which is almost identical with that of the mature fruit.

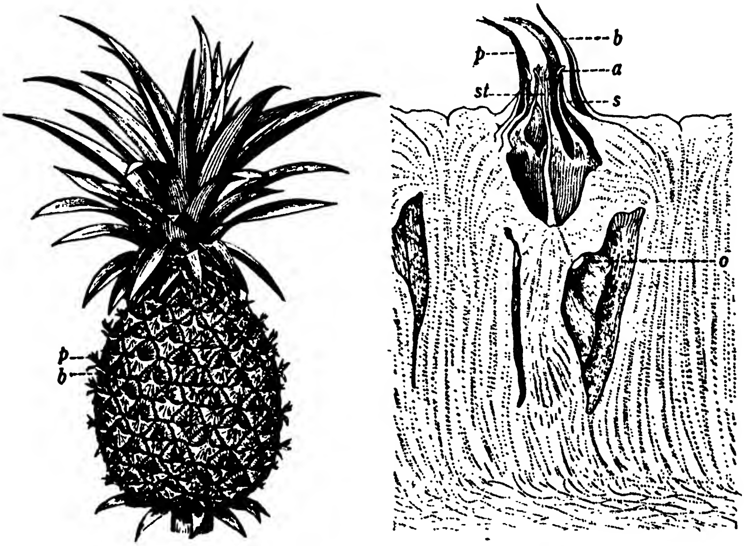


FIG. 330. Collective fruit of pineapple

Left, mature fruit. Note that the fruit is made up of a number of fused fruits and that each of these is subtended by a bract (*b*). In this pineapple the remains of the three petals show plainly (*p*), but in many pineapples they disappear before the fruit is ripe. Right, a section showing a single fruit and portions of two adjacent fruits. The parts of the flower show plainly in this figure: *b*, bract; *s*, sepal; *a*, anther of one of the stamens; *p*, petal; *st*, style; *o*, abortive ovule. The chief difference, except for size, between the appearance of the inflorescence in the flowering stage and of the mature fruit is in the petals. In the flowering stage the flowers open a few at a time progressively from base to apex, and the three purple petals, while not conspicuous, are plainly visible. In the mature fruit either they are shriveled, as in the specimen illustrated, or they have disappeared

When several separate ovaries in one flower unite to produce a fruit, this fruit is known as an *aggregate* fruit (Figs. 332, 333; compare Fig. 334).

Composition of fruits. Some fruits are produced by superior ovaries, and others by inferior ones. An ovary is said to be *superior* when the point of attachment of the calyx and corolla is below the ovary (Figs. 283, 284, 300), and *inferior* when the point of attachment is above the ovary (Figs. 291, 316, 299), as in epigynous flowers. In the latter case the torus may be considered as having a bottlelike form, at the summit of which the calyx, corolla, and stamens are attached. In such cases the torus takes part in the formation of the fruit. When the fruit is derived from a superior ovary, the remains of the calyx can frequently be found at

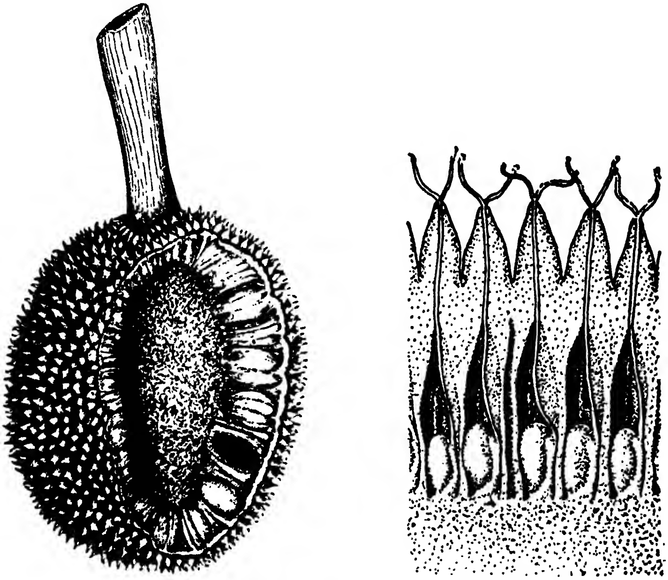


FIG. 331. Collective fruit of breadfruit (*Artocarpus communis*)

Left, mature fruit with some of the seed-containing part removed to show structure (× ⅓). Right, section of inflorescence at time of flowering. At this stage the ovaries are completely fused together and the form of the inflorescence is almost exactly like that of the mature fruit. Note ovaries with styles running outward and each terminating in two stigmas

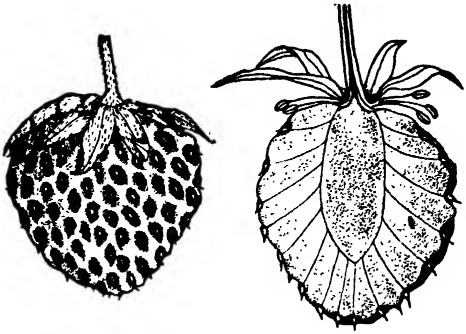


FIG. 332. Aggregate fruit of strawberry

The fleshy portion is an enlarged torus. Compare Fig. 302. (× 1)

the base of the fruit, as in the grapefruit (Fig. 335) and orange. When the ovary is inferior, the remains of the calyx can sometimes be plainly seen at the apex of the fruit (Fig. 336). In the flower of the apple five imperfectly fused carpels are more or less enclosed in a cup-like torus. During the formation of the fruit the carpels fuse with the torus and form the characteristic apple fruit. In this (Fig. 337) the ovary is represented by the core and the torus by

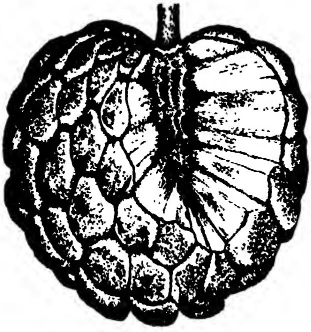


FIG. 333. Aggregate fruit of sugar apple (*Anona squamosa*), with some sections removed to show structure

The sugar apple is a native of tropical America now widely cultivated in tropical countries. It is an edible fruit. It has an excellent mild flavor, but is very seedy, as each section contains a large seed. (× ½)

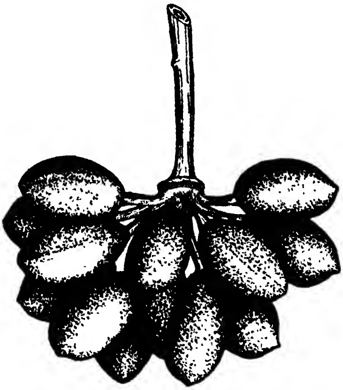


FIG. 334. Separate fruits of ylang-ylang (*Canangium odoratum*) formed from separate ovaries in the same flower

This plant belongs to the same family as the sugar apple, Fig. 333, and the arrangement of the ovaries in the flower is very similar, but the development of the fruit is not. Ylang-ylang flowers yield one of the best and most valuable perfumes. (× ⅔)

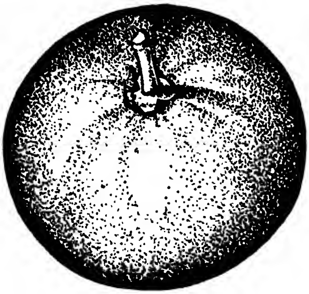


Fig. 335. Grapefruit developed from superior ovary

Note remains of calyx at base of fruit. (× $\frac{2}{5}$)

the surrounding fleshy portion. The rose fruit (Fig. 338) is an aggregate fruit in which the torus surrounds distinct individual fruits just as the torus in the flower surrounded the individual ovaries (Fig. 303).

In many fleshy fruits the fleshy part is the ovary wall or a portion of it (Figs. 354, 356). In others it consists entirely of the enlarged torus (Fig. 332). In quite a number of fruits the fleshy portion is an *aril,* an outgrowth from the funiculus, which in some cases, as in the litchi (Fig. 339), completely surrounds the seed. In the litchi the aril forms a thick translucent pulp. The rambutan of the Malay Peninsula is closely related to the litchi and has a similar structure.

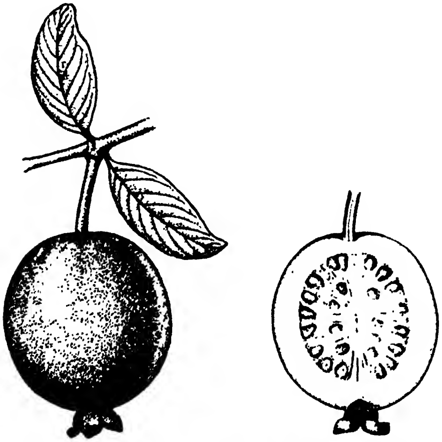


Fig. 336. Berry of guava developed from an inferior ovary

The guava is a native of tropical America, but is widely distributed and cultivated in tropical countries. Although it is very seedy it is a favorite fruit with natives of tropical countries. It is much used in making guava jelly. (× $\frac{1}{4}$)

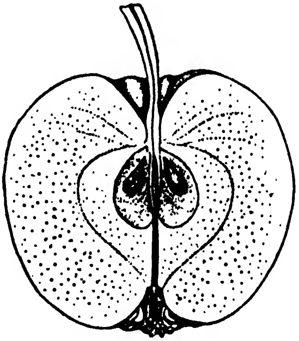


Fig. 337. Cross section of an apple fruit, showing ripened ovary surrounded by the enlarged torus

The apple is grown only in temperate countries, but owing to its excellent shipping qualities it is widely known and eaten in the tropics. Compare Fig. 299. (× $\frac{1}{2}$)

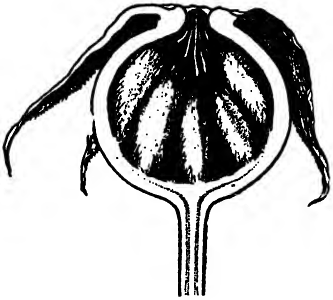


FIG. 338. **Fruit of rose**

The flask-shaped torus surrounds a number of individual fruits just as the torus in the flower surrounded the individual pistils (Fig. 303)

The nutmeg is a seed partially enclosed in a fleshy aril, which when dried is the mace of commerce. The nutmeg and mace are surrounded by a pericarp which splits into two valves when the fruit is mature (Fig. 340).

In the cashew (Fig. 341) the mature fruit consists of a fleshy portion which is formed largely from the stalk of the fruit, but in which the torus takes part. At the tip of the fleshy portion is a true nut developed from the ovary.

In the lime the fleshy portion is formed by hairlike outgrowths from the walls of the ovary (Fig. 342). In some cases the fleshy part is composed of the outer coverings of the seeds (Figs. 378, 343). In the mulberry (Fig. 329) the fleshy part consists largely of thickened, fleshy calyx lobes; see also Fig. 344. The collective fruit of the pineapple is composed of a central axis and numerous flowers which become fleshy. The fig is a hollow pear-shaped inflorescence on the inside of which are many flowers (Fig. 345). These flowers are developed into many small, seedlike fruits which are often mistaken for seeds.

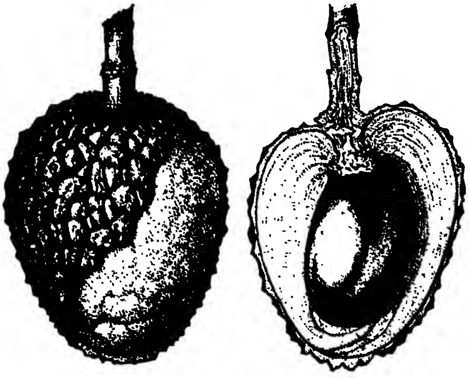


FIG. 339. **Fruit of litchi**

Left, a fruit from which a part of the pericarp has been removed to show the translucent pulpy aril; right, a section of the fruit showing the large shiny seed surrounded by the pulpy aril growing from the funiculus and this enclosed in a thin pericarp. (× ½). The litchi is a delicious fruit; it is widely used in China and has been introduced into other subtropical countries. In the dried litchi the pulp has shrunk away from the pericarp

Classification of fruits. Fruits are usually divided into two classes, *dry* and *fleshy*. The dry fruits may be subdivided into *dehiscent* fruits, or *capsules*, and *indehiscent* fruits. Dehiscent fruits are those which open at maturity so that their seeds can escape, while indehiscent ones are those which do not open. Indehiscent fruits may be further subdivided into *achenial* and *schizocarpic* fruits. The fleshy fruits may be divided into *drupes* and *berries*.

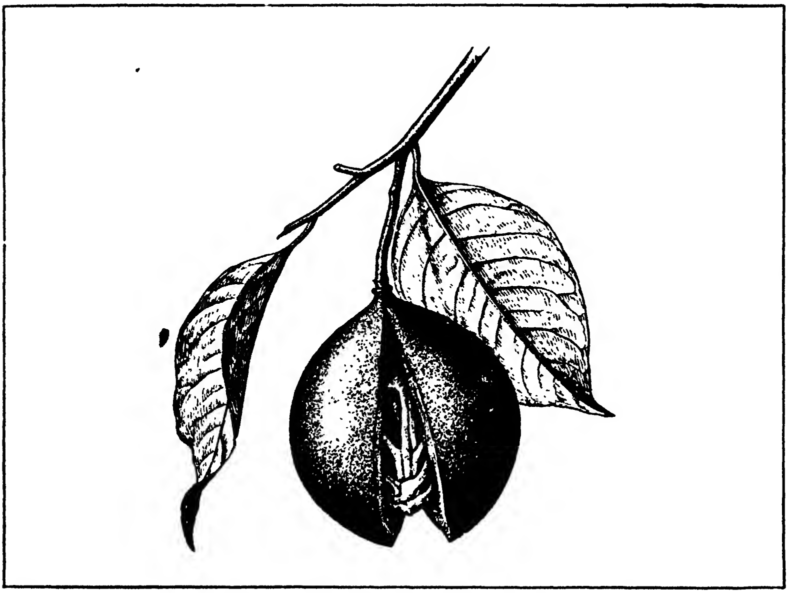


FIG. 340. Fruit of *Myristica fragrans*

The single seed is a nutmeg. This is more or less surrounded by an aril, which when dried is the mace of commerce. The pericarp when ripe splits into two valves as shown in the illustration. (× ½)

Capsules. Dry, several-seeded to many-seeded, dehiscent fruits are known as capsules. Capsules are of many shapes, and they open in many different ways (Figs. 346–350, 362, 372, 373). The *legume*, or *pod*, and the *follicle* are special kinds of capsules. The follicle and the legume are each derived from an ovary composed of a single carpel. The follicle splits along one side only (Fig. 348), while the legume, which is the characteristic fruit of the pea or bean family, usually splits along two edges (Fig. 349).

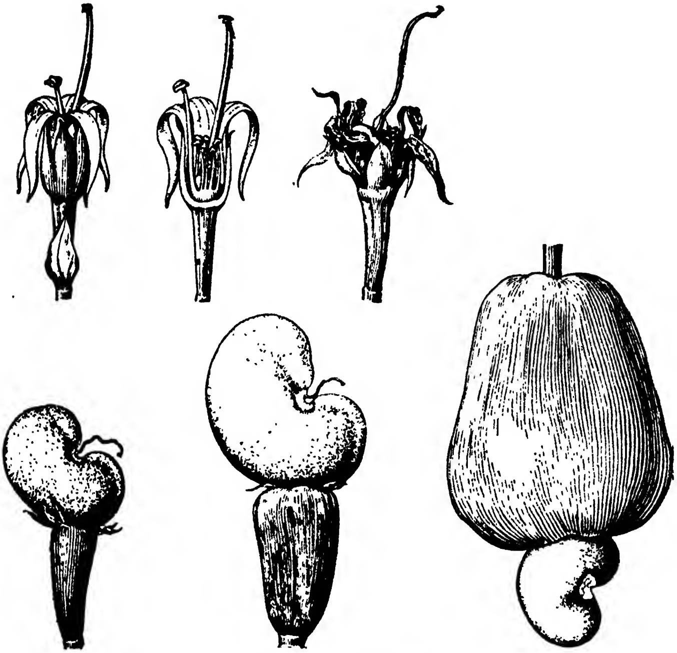


Fig. 341. Development of cashew fruit

Upper left, flower; center, section of a flower, showing ovary surrounded by stamens, one of which is much larger than the others; right, the fertilized ovary has already begun to enlarge; below, further development of nut from ovary and of fleshy portion from stalk and torus

Achenial fruits. An *achene* is a small, dry, indehiscent, one-seeded fruit (Fig. 351). The achenes of the sunflower are sold under the name of *sunflower seed.* The *caryopsis,* or *grain,* differs from the achene in that the pericarp, or wall of the fruit, is fused with the testa (the outer covering of the seed). The grain is the typical fruit of the grasses, and its structure can be observed very clearly in corn (Fig. 388). The *samara,* or *key,* is a winged achene (Fig. 352). The *nut* is a one-seeded, usually inde-

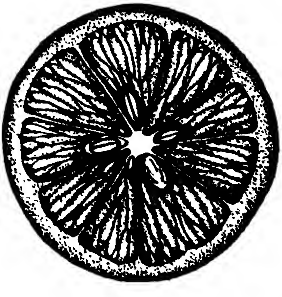


Fig. 342. Cross section of fruit of lime

The fleshy part consists of hairs from ovary walls. (× 1) hiscent fruit (Fig. 341) in which the pericarp, the wall of the fruit, is hard. Many structures which are popularly called nuts do not fit this description.

Schizocarpic fruits. These are dry fruits which split up into a number of one-seeded, usually indehiscent parts (Fig. 353), as in the castor-oil plant.

Drupes. A drupe is a fruit in which the endocarp is hard and the mesocarp fleshy or fibrous (Figs. 354, 355, 356, 389). Many structures popularly known as nuts are composed of the endocarps and the seeds of drupes; the walnut and the almond are examples. The most familiar drupes have only one seed; but in the huckleberry we see a drupe which has ten stones arranged in a circle.

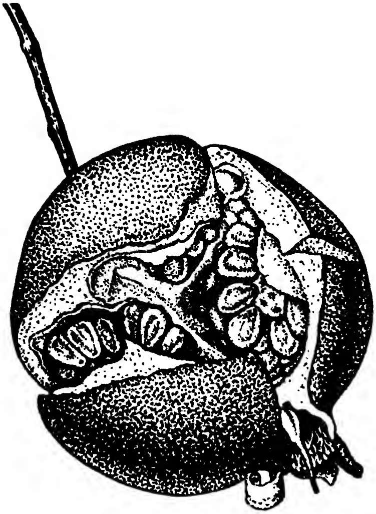


Fig. 343. Pomegranate (*Punica granatum*)

The pomegranate has many seeds, each surrounded by an edible pulp, which is a portion of the testa that is fleshy in the mature fruit

Berries. Fleshy, indehiscent, few-seeded to many-seeded fruits are known as berries (Figs. 357, 358). The word *berry*, like

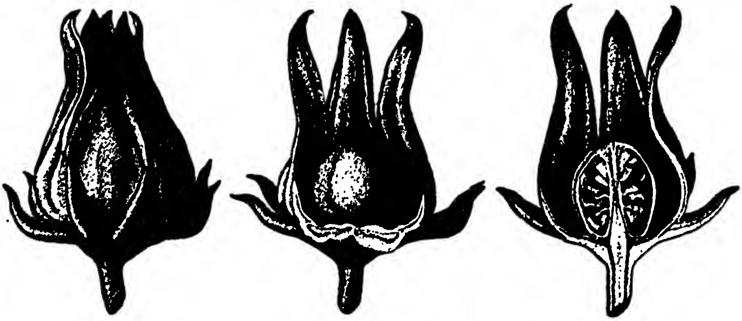


Fig. 344. Fruit of roselle

The edible part of this fruit consists of the fleshy calyx and bracts; the fruit proper is hard and dry. Left, entire fruit; center, part of fleshy calyx removed; right, section through hard dry fruit, showing hard seed

the word *fruit* or the word *nut*, has thus very different botanical and popular meanings. The date is a one-seeded berry, as the "stone" is the seed and not the endocarp. Tomatoes, grapes, and bananas are berries, while oranges, cucumbers (Fig. 358), melons, and apples are examples of special classes of berries.

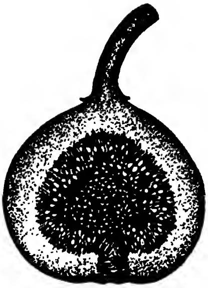


Fig. 345. Collective fruit of fig

The separate fruits are surrounded by an enlarged stem. (× 1)

Classification inexact. In discussing the different types of fruits it is convenient to use some such classification as that given above, although it should be realized that any classification must be arbitrary and in many cases inexact. The fruit of the balsam (Fig. 382) is a somewhat fleshy capsule. Many capsules have no regular method of dehiscence.

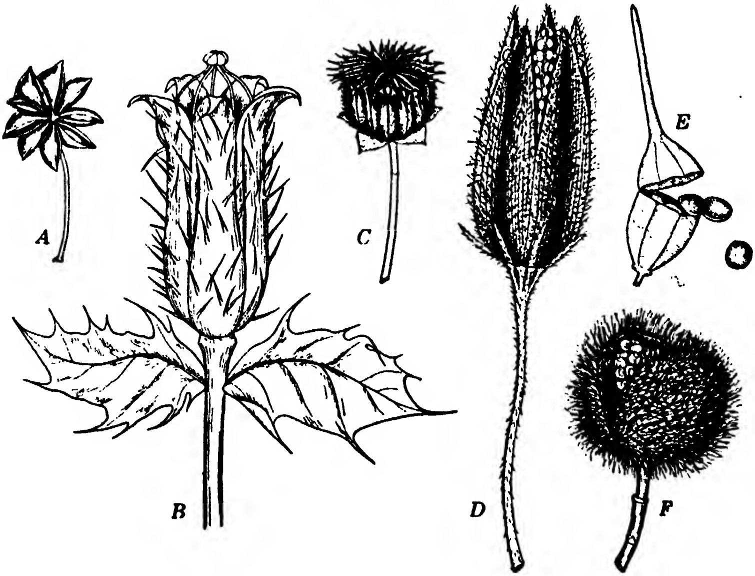


Fig. 346. Various forms of capsules

A, *Illicium verum* (× ½); *B*, *Argemone mexicana* (× ½); *C*, *Abutilon indicum* (× ½); *D*, *Abelmoschus moschatus* (× ½); *E*, *Celosia argentea* (× 4); *F*, *Bixa orellana* (× ½)

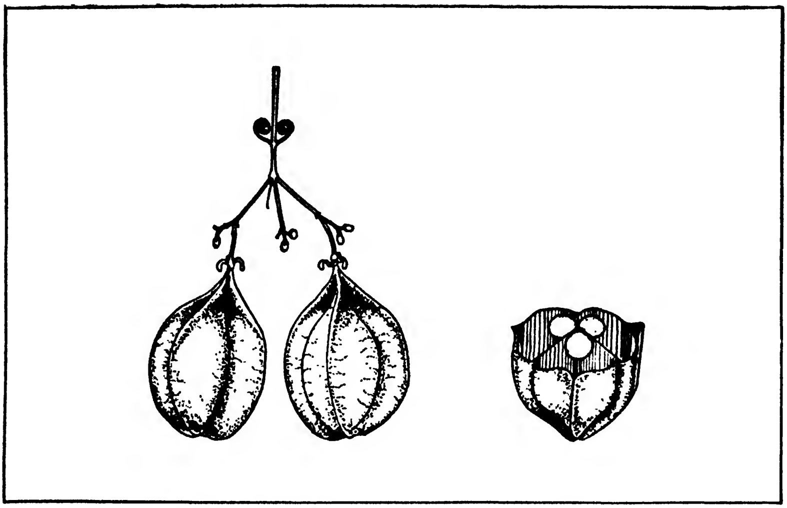


Fig. 347. Inflated capsule of *Cardiospermum halicacabum.* (× ⅔)

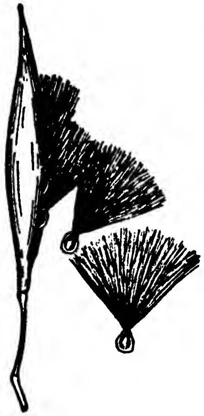


Fig. 348. Follicle of a milkweed (*Asclepias curassavica*), showing liberation of seeds with their hairy appendages. (× ½)

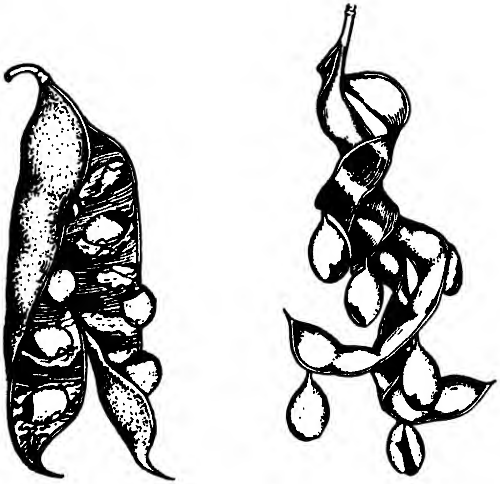


Fig. 349. Unusual types of pods

Left, *Abrus precatorius* (× 1); the seeds are very hard and bright red, each with a black spot at one end, and, although indigestible, are dispersed by birds. Right, *Pithecolobium dulce* (× ½); the seeds have a white fleshy covering and are dispersed by birds

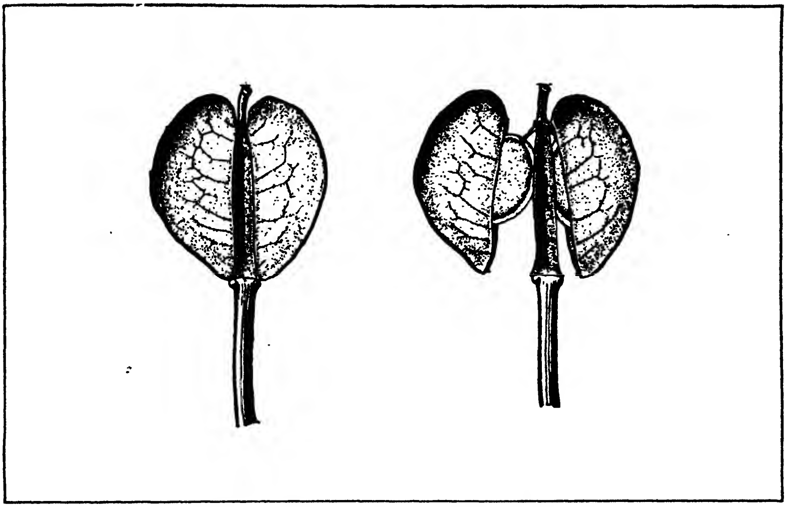


Fig. 350. Two-valved capsule of candytuft

This type of capsule is known as a *silicle*. If it were long and slender, as in cabbage or mustard, it would be a *silique*. (× 3)

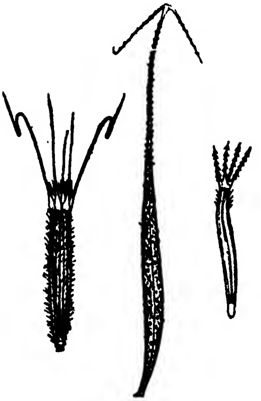


Fig. 351. Achenes of *Elephantopus*, *Cosmos*, and *Bidens* (beggar-ticks)

These are dispersed by adhering to animals. (× 2½)

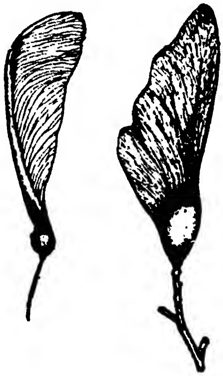


Fig. 352. Samaras of *Securidaca corymbosa* and *Tarrietia sylvatica*. (× ⅜)

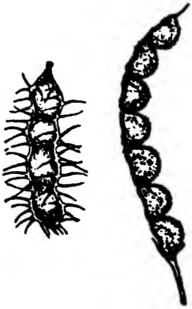


Fig. 353. Schizocarpic pods of sensitive plant (*Mimosa pudica*) and tick trefoil (*Desmodium gangeticum*). (× 1)

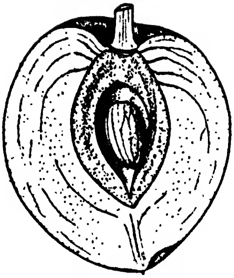


Fig. 354. Longitudinal section of drupe of peach. (× ½)

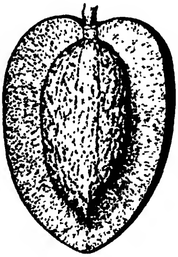


Fig. 355. Drupe of olive. (× 1½)

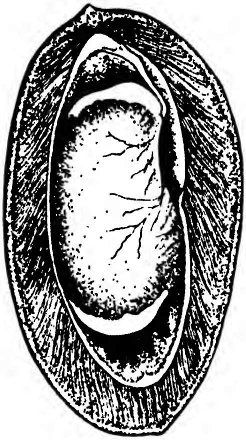


Fig. 356. Longitudinal section of drupe of mango (*Mangifera indica*). (× ½)

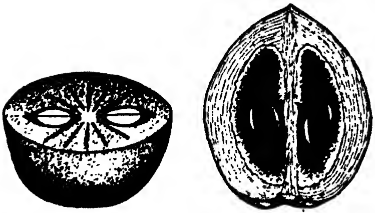


Fig. 357. Berry of sapodilla or chico (*Achras sapota*). (× ½)

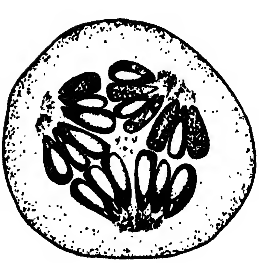


Fig. 358. Cross section of berry of cucumber. (× ½)

THE SEED

A *seed* is a structure developed from an ovule. It consists of an embryo, stored food which may be either in or around the embryo, and one or two coverings called *seed coats* (Figs. 359, 360).

The embryo. This consists of a small undeveloped shoot called the *plumule*, a cylindric structure known as the *radicle*, which will develop into a root, and one or two large leaves which are the *cotyledons*, or seed leaves (Figs. 359, 361). Plants with one cotyledon (Figs. 388, 389) are called *monocotyledons*; those with two (Fig. 359) are called *dicotyledons*.

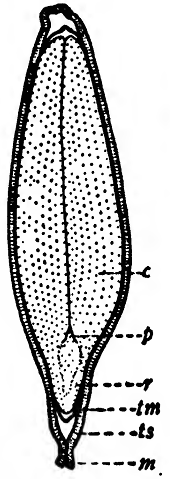


FIG. 359. Longitudinal section of squash seed

c, cotyledon; *p*, plumule; *r*, radicle; *tm*, tegument; *ts*, testa; *m*, micropyle. (× 3)

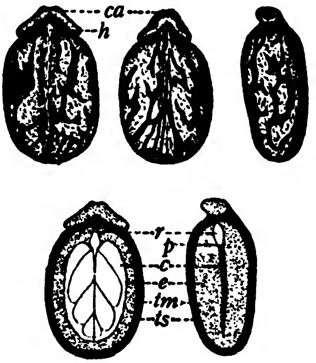


FIG. 360. Ventral, dorsal, and lateral views of seed of castor-oil plant (*Ricinus communis*), with section of seed

Above: *ca*, caruncle; *h*, hilum. Below: at left, section cut from side to side; at right, section cut perpendicular to dorsal surface; *r*, radicle; *p*, plumule; *c*, cotyledon; *e*, endosperm; *tm*, tegument; *ts*, testa. (× 2)

Endosperm. In some seeds, such as the squash seed and the lima bean, the cotyledons are large and fleshy and are filled with stored food (Figs. 359, 361). In others the cotyledons are thin and are surrounded by a mass of food-storage tissue, the *endosperm*, as in the seed of the castor-oil plant shown in Fig. 360. Most seeds of flowering plants contain an endosperm at some stage of their development, and the food stored in this endosperm is absorbed by the cotyledons. In many cases the endosperm is completely absorbed before the seeds are mature, and in such cases the ripe seed does not contain an endosperm (Figs. 359, 361). In other cases much of the food material in the endosperm is not absorbed by the cotyledons until the seeds germinate. In these cases the mature seed contains an endosperm.

Perisperm. In the ovule the embryo sac is surrounded by the nucellus. Just as the embryo absorbs food material from the endosperm, so the endosperm absorbs food material from the nucellus. In most seeds the nucellus is entirely absorbed before the seed is ripe, and even the inner integument may be so absorbed. In some cases, however, the ripe seed contains an embryo surrounded by the endosperm, and this, in turn, by the nucellus. When the nucellus remains in the mature seed it is known as perisperm.

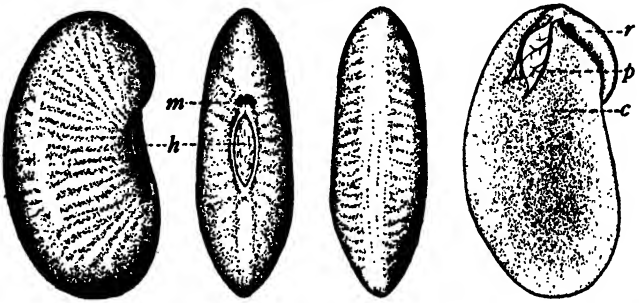


Fig. 361. Lima bean, showing lateral, ventral, and dorsal views and embryo

At left: *m*, micropyle; *h*, hilum. At right: embryo with seed coat and one cotyledon removed; *r*, radicle; *p*, plumule; *c*, cotyledon. (× 1½)

Seed coats. The seed coats are derived from the integuments of the ovule. The outer seed coat, or *testa*, develops from the outer integument. The testa is usually thick and hard (Fig. 359). The inner seed coat, or *tegmen*, is usually thin (Fig. 359). This is derived from the inner integument. In some cases there is only one seed coat.

Hilum. On the testa there is a scar marking the place where the funiculus was attached to the ovule (Fig. 361). This scar is known as the hilum.

Micropyle. The testa is pierced by a small hole, the micropyle (Fig. 361), which is the same structure as the micropyle in the ovule. The tip of the radicle points toward the micropyle.

SEED DISPERSAL

We have seen that the seed consists of an embryo, stored food material, and a protective covering. The embryo is capable of growing into a plant, and the stored food material furnishes it with a supply of food for its growth in the period before it has become established. Most seeds are also provided with some means of dispersal. Without this the great majority of seeds would fall under the parent plant and not be carried to a location favorable to germination and growth. The mechanism of dissemination may be a part of the seed itself or may belong to surrounding portions of the fruit. The principal agencies by which seeds are dispersed are wind, water, animals, and explosive mechanisms.

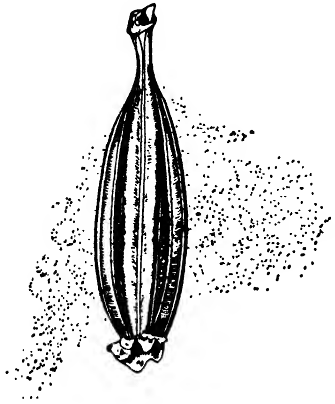


FIG. 362. Capsule of an orchid (*Cymbidium finlaysonianum*) open and with minute seeds being scattered by the wind. (× ½)

Dispersal by wind. Either the whole fruit or the individual seeds may be suited to dispersal by wind. Seeds that are thus disseminated are characteristically light. The means of adaptation to wind dispersal may be grouped under the headings of *minute seeds*, *flattened fruits or seeds*, *winglike outgrowths*, *feathery appendages*, and the so-called *censer mechanisms*.

Minute seeds. The seeds of orchids are very small and, besides, have a light, inflated outer covering. These dustlike seeds can be blown by the wind for great distances (Fig. 362).

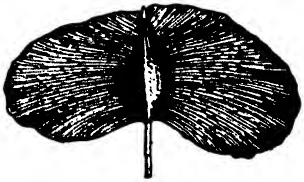


FIG. 363. Flattened wing fruit of *Terminalia calamansanay*. (× ½)

Wings. In many cases seeds, and in others whole fruits, are flattened or have winglike outgrowths (Figs. 363, 364, 365, 368; compare Figs. 367, 369), or they may be both flattened and

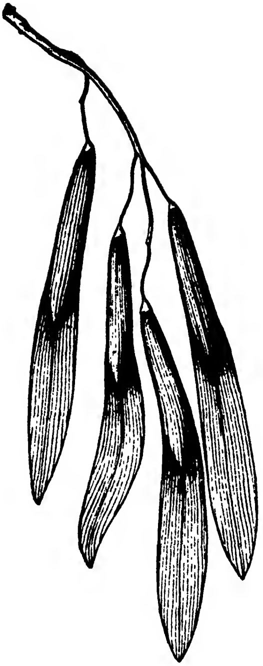


Fig. 364. Flattened fruits of ash, adapted to wind dispersal. (× 1½)

winged (Fig. 366). This type of structure results in the scattering of the seed by the wind.

Feathery appendages. Seeds (Fig. 348) or fruits (Figs. 370, 371) may have feathery appendages which greatly increase their buoyancy, so that they are frequently carried by the wind to considerable altitudes. These feathery appendages are very characteristic of the seeds of milkweeds (Fig. 348) and of the achenes of many composites (Fig. 370). Commercial cotton consists of trichomes which grow from the epidermal cells of the seed of the cotton plant. These trichomes form a flossy mass round the seed.

Censer mechanisms. The capsules of many plants open in such a way that the seeds can escape only when the capsules are violently shaken, as by a strong wind (Figs. 346, 372, 373). This has a tendency to scatter the seeds. The seeds may in addition have a flat shape (Fig. 372) or winged outgrowths; and as they are likely to escape when there is a strong wind, they may be blown for considerable distances.

Dispersal by water. Adaptations for dispersal by water are not so common as are those for dispersal by wind, but the former occur in many seashore and aquatic plants. Either the whole fruit or the seed may be adapted for floating. The pericarp of a fruit may be composed of light tissue (Fig. 374) or the fruit may be inflated (Fig. 375).

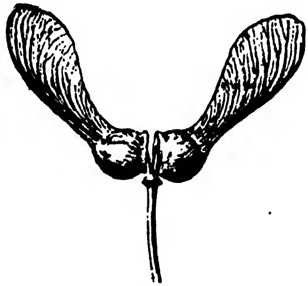


Fig. 365. Schizocarp of maple with flattened wings

After Faguet

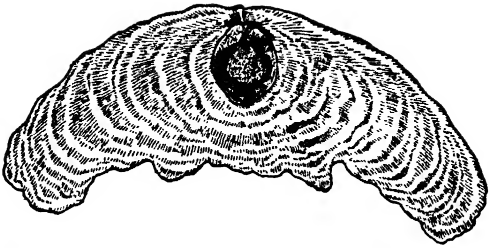


Fig. 366. Flattened seed of *Macrozanonia* with large, papery wing. (× $\frac{5}{12}$)

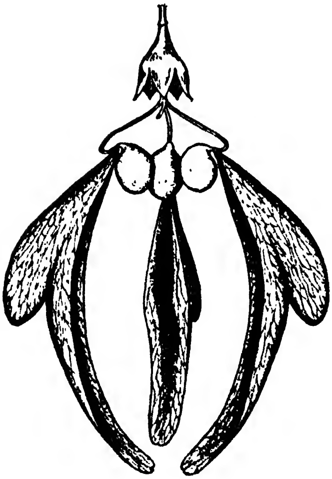


Fig. 367. Follicles of *Pterocymbium tinctorium*, adapted to wind dispersal. (× ½)

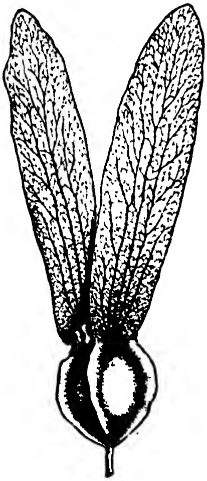


Fig. 368. Fruit of *Dipterocarpus grandiflorus* with wings formed by enlarged calyx lobes. (× ⅓)

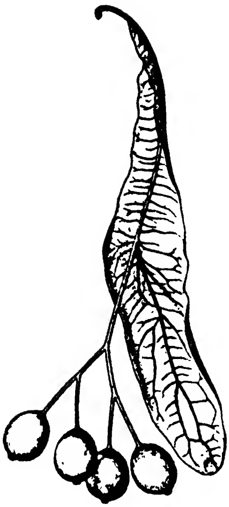


Fig. 369. **Fruit of linden, adapted to wind dispersal by being attached to a specialized leaf (bract).** (× ⅔)

The coconut (Fig. 389) is an excellent example of a fruit with a light pericarp. Floating seeds may likewise contain either a mass of light tissue or large air spaces (Fig. 376). In the lotus fruit (Fig. 377) the torus is a greatly enlarged mass of loose, air-filled tissue which floats readily, while the individual fruits are also adapted for floating. Many seeds that are not especially fitted for floating may occasionally float for short distances, or seeds that by themselves would not float may be carried in floating debris.

Dispersal by animals. Seeds that are adapted for dispersal by animals are disseminated in two general ways: in the case of fleshy fruits a portion of the fruit is eaten by the animal (Fig. 378), while many dry fruits adhere to animals.

Fleshy fruits. Fleshy fruits are generally adapted to being eaten by animals. Such fruits are usually constructed so that the fleshy part may be eaten without injury to the seed. In many cases the seed coat is very hard, while in drupes the seed is protected by the stony endocarp. Owing to this protection a seed may pass without injury through the digestive tract of an animal. Birds are particularly prominent in disseminating the seeds of fleshy fruits. Sometimes they eat the fleshy portion of a fruit and throw the seeds away. Dry fruits are

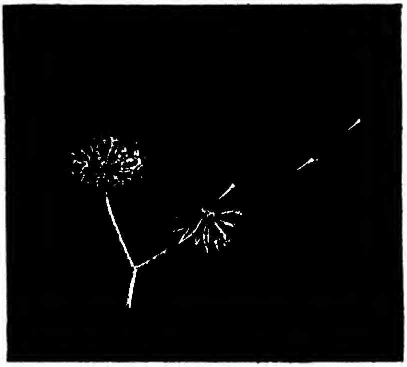


Fig. 370. **Fruits (achenes) of ironweed (*Vernonia*), suited to dispersal by wind on account of their hairy appendages**

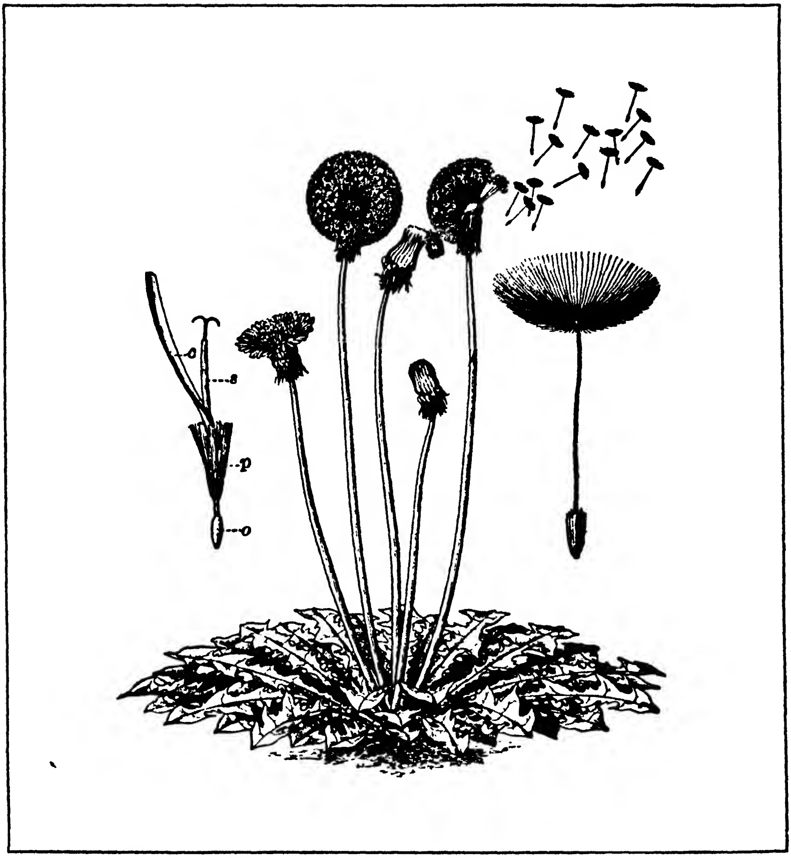


Fig. 371. Dandelion (*Taraxacum*)

The center figure shows a flower bud, a flower head, a flower head after fertilization, a ripe head with seed, and dispersal of seeds by the wind. To the left is a single flower: *o*, the ovary; *p*, pappus consisting of a circle of hairs which are really the calyx; *c*, strap-shaped corolla; *s*, united stamens enclosing the style, which terminates in two stigmas. To the right is a single mature fruit. Note that the "parachute" which is responsible for its being dispersed by the wind is derived from the calyx

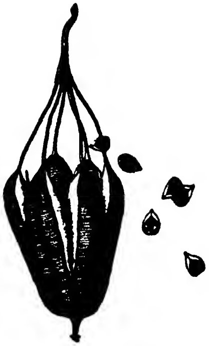


Fig. 372. Capsule of *Aristolochia elegans*

It hangs in such a position that the seeds are liberated only when it is shaken by the wind. The flattened seeds are adapted to wind dispersal. (× ½)

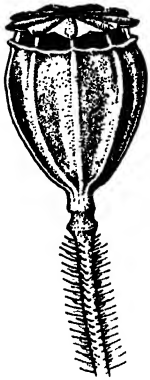


Fig. 373. Capsule of poppy

The seeds are liberated only when the capsule is shaken rather violently. (× 2½)

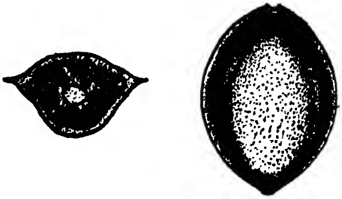


Fig. 374. Fruit of *Terminalia catappa*, adapted to dissemination by water by having a thick fibrous husk. (× ½)

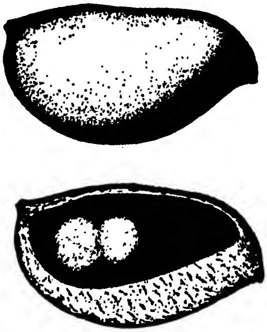


Fig. 375. Fruit of *Heritiera littoralis*, adapted to dissemination by water by having a thick fibrous husk enclosing an air cavity. (× ½)

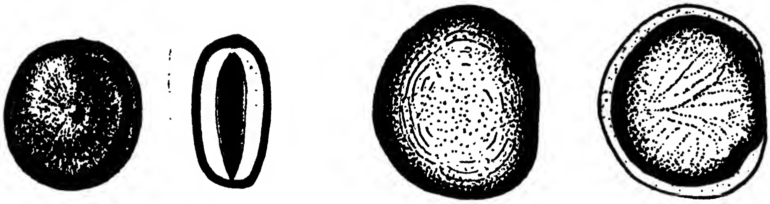


Fig. 376. Seeds of *Entada scandens* (× ½) and *Mucuna gigantea* (× 1)

These are adapted to dispersal by water by having an impervious seed coat and by containing an air cavity (in the first case between the cotyledons, and in the second around the embryo)

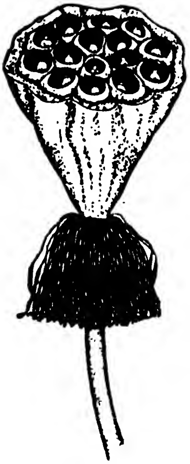


Fig. 377. Fruit of *Nelumbium nelumbo*

Below are the remains of the stamens. The large part above is the enlarged torus, the fruits being in depressions in the torus. The fruits float, and, besides, the enlarged torus is replete with air cavities and is very buoyant. (× ½)

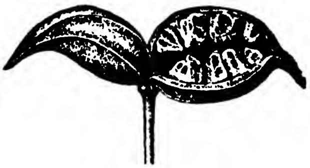


Fig. 378. Double follicle of *Tabernaemontana pandacaqui*

The follicle to the right has opened. The seeds are suited to dispersal by animals by having brilliantly colored fleshy coverings. (× ½)

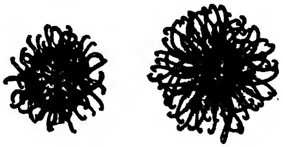


Fig. 379. Fruits adapted to dissemination by having hooks which adhere to animals

Left, *Triumfetta bartramia* (× 2); right, *Triumfetta annua* (× 1) often carried off for food by seed-eating animals which lose them in one way or another and leave them to grow.

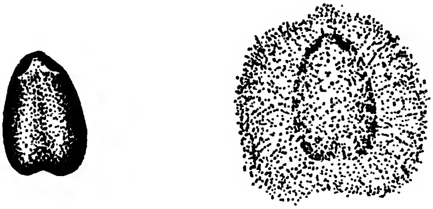


Fig. 380. Seed of *Hyptis suaveolens*, adapted to dissemination by animals by having a mucilaginous covering which swells and is very sticky when wet

Left, dry seed; right, wet seed. (× 4)

Adhesive fruits. Many dry fruits have hooklike appendages (Figs. 351, 353, 379) which are particularly fitted for grasping the hair of animals. Animals to which the fruits adhere carry them about and thus distribute the seeds. In a similar way fruits may adhere to clothing and thus be disseminated by man. Some seeds and fruits have a sticky covering which will adhere to the hair of an animal (Fig. 380). Fruits of forget-me-nots adhere by sticky hooklike appendages (Fig. 381). Feathery appendages are usually capable of adhering to fur as well as of flying on the wind.

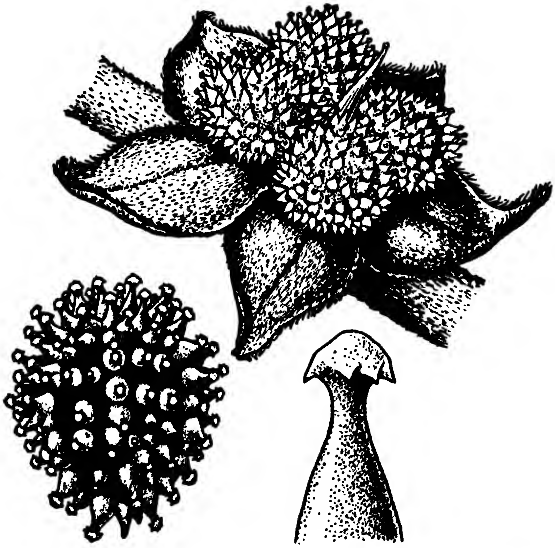


Fig. 381. Fruit of Chinese forget-me-not. (× 4)

Minute seeds. Many plants have minute seeds which are disseminated by being caught in mud that adheres to the feet or other parts of birds or other animals.

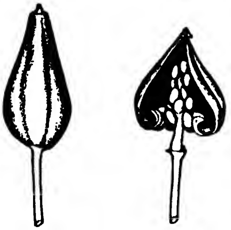


FIG. 382. Fruit of *Impatiens balsamina*, which explodes and scatters the seeds. (× 1)

Dispersal by explosive mechanism. Many fruits are so constructed that they explode when ripe and scatter the seeds. This method of dispersal is frequently conspicuous in members of the bean family, where the explosive forces are due to stresses arising from the drying of the valves of the pod. The balsam has somewhat fleshy capsules which are very turgid. When these are disturbed by contact the segments of the pericarps roll up with considerable force and in such a way that they scatter the seeds (Fig. 382). An unusual explosive mechanism is found in the squirting cucumber (Fig. 383).

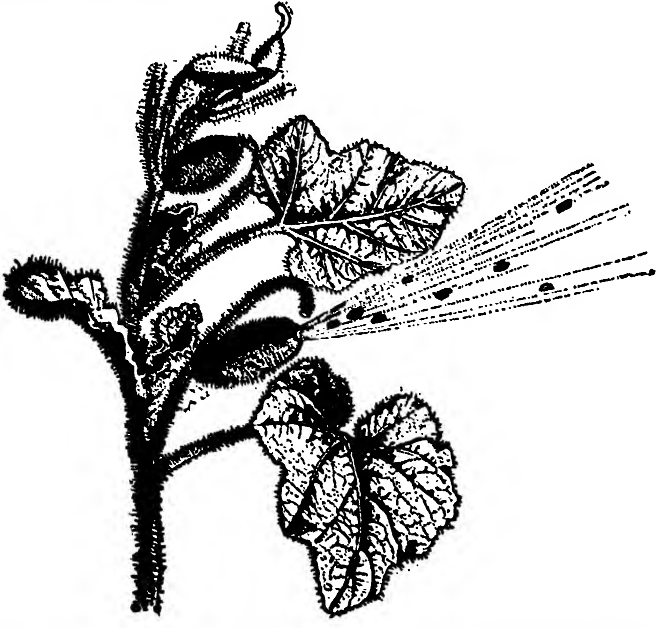


FIG. 383. Seed dispersal in the squirting cucumber (*Ecballium elaterium*)

After Baillon

Burying. The fruits of the peanut are borne in a very unusual manner. Instead of being developed above ground they are buried into the soil (Fig. 384).

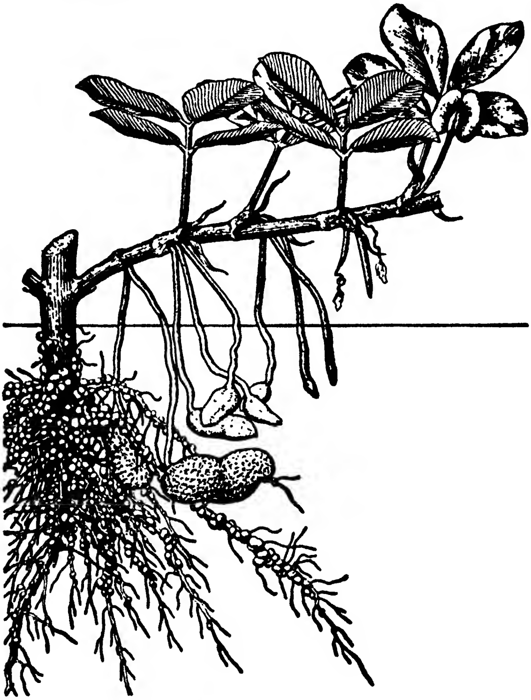


FIG. 384. Peanut, showing development of fruit

The flower of the peanut has a very long style and a long calyx tube at the top of which are found the calyx lobes, the petals, and the attachment of the stamens. After fertilization, the flower withers, the stalk turns downward, and the fruit elongates greatly without broadening until its tip, in which are the ovules, has been pushed into the soil; then this tip expands into the well-known "nut." The nodules on the roots contain nitrogen-fixing bacteria

GERMINATION OF SEED

Definition. The development of the seed into a young plant is called *germination.* A seed is said to have germinated when the radicle and plumule have reached out of the seed coat, but germination is not complete until the seedling has become established and is independent of the food supply stored in the seed.

Period of rest. Seeds usually undergo a period of rest before germinating. The length of this period varies greatly in different species, and in some cases it is altogether lacking. In the mangrove-swamp species of the family *Rhizophoraceae* the seeds germinate without falling from the tree. The first sign of the germination of such seeds is the projection of the long, slender radicle from the fruit (Fig. 385). After the radicle has grown to a considerable length the seedling drops, radicle down, the tip of the radicle is usually driven into the mud, and the growth of the seedling continues (Fig. 386). While thus the growth of some embryos apparently ceases for only a very short period, if at all, most seeds in their ripening lose a considerable part of their water and become comparatively dry. Under such conditions life processes continue at a very slow rate, and for practical purposes the seed is in a condition of rest. Many seeds will not begin to germinate until they have been in the state of rest for a considerable length of time, while others will germinate almost immediately.

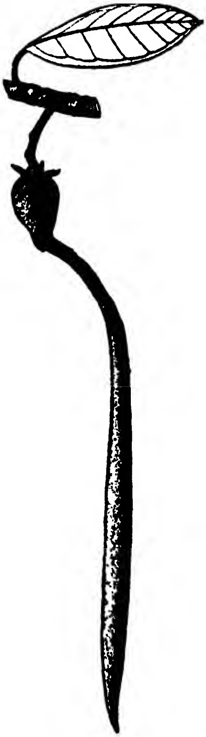


Fig. 385. Germinating seedling of *Rhizophora* projecting from a fruit that is still attached to a tree. (× ⅓)

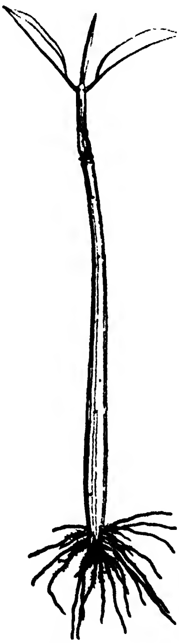


Fig. 386. Seedling of *Rhizophora* after dropping from the tree and taking root. (× ⅙)

A period during which seeds will not germinate is frequently of great advantage, particularly when the seeds are formed at the end of the growing season. In many regions the year is divided into a season which is favorable and another which is unfavorable to growth. Unfavorable seasons may be due to either very cold or very dry weather. It is obvious that if seeds began to germinate at the beginning of a long cold or long dry season, the seedlings would start under very disadvantageous conditions and would stand little chance of surviving. In regions where conditions are favorable to growth throughout the year, a prolonged period of

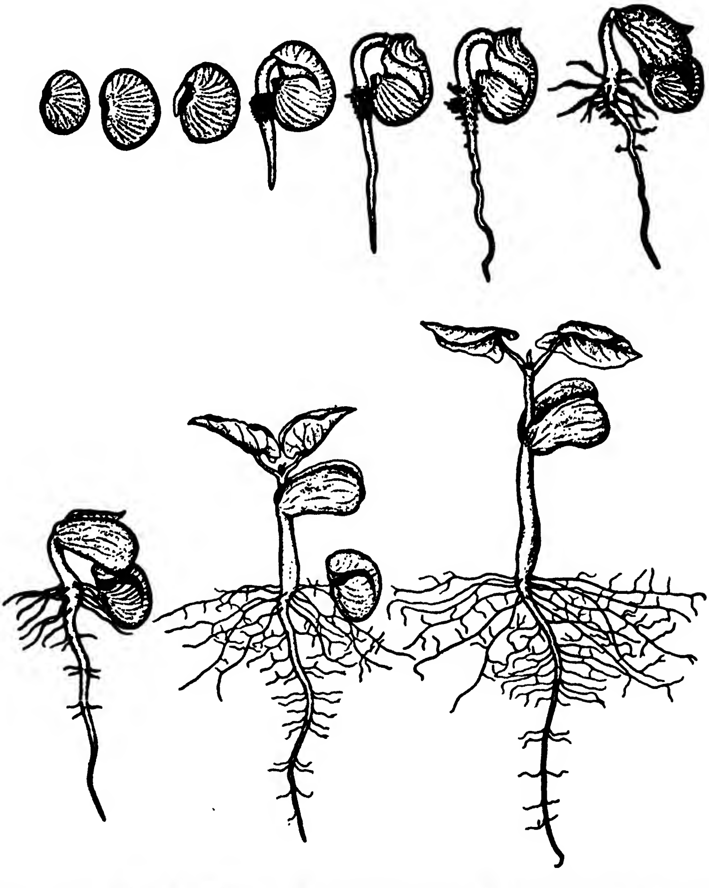


Fig. 387. Successive stages in the germination of lima bean (*Phaseolus lunatus*)

The cotyledons are carried up into the air and furnish food for the embryo, but do not become leaflike. (× $\frac{1}{3}$)

rest is unnecessary. The seeds of many plants that are natives of moist tropical regions germinate almost immediately, and if stored they lose their capacity for germination in a very short time.

Many seeds have hard seed coats which are impervious to water; such seeds will not germinate until the seed coats have rotted or have been injured in some other way. This explains why the germination of many seeds is hastened by making holes in the seed coats. A period of rest is, however, not confined to seeds with impervious coats, as the necessity for a period of rest is often characteristic of the seeds themselves. Such seeds seem to need some metabolic change to make them ready for germination.

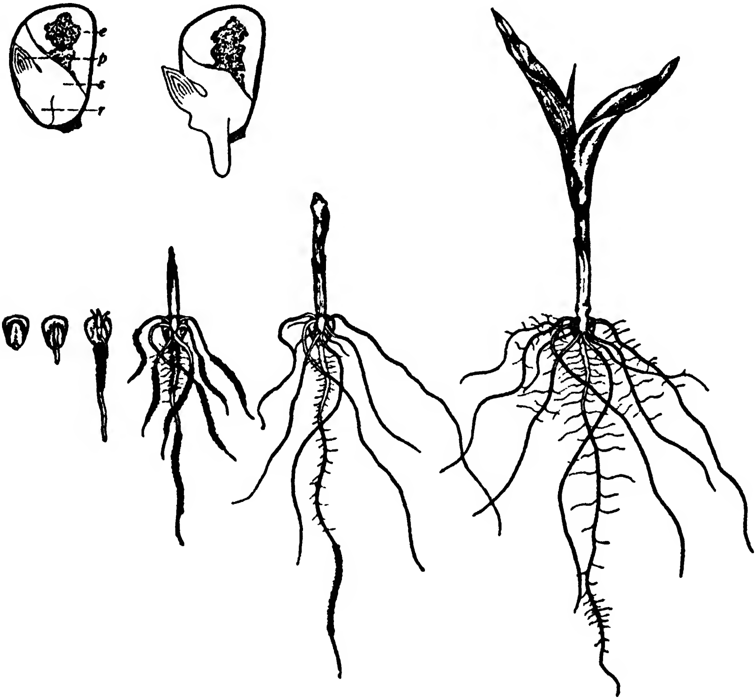


Fig. 388. Seed and germination of seedling of Indian corn

Above, section of ungerminated seed and a seed in which the plumule and radicle are pushing out: *e*, endosperm; *s*, cotyledon, or scutellum; *p*, plumule; *r*, radicle (× 1½). Below, germination of seed (× ⅖)

Seeds in a dormant condition can withstand much greater extremes of heat and cold than can seedlings or mature plants.

Conditions for germination. Germination is really a process of growth, and the conditions that are necessary for germination are essentially the same as those that are required for other forms of growth. Growth is dependent on a supply of food, water, and oxygen, and a suitable temperature. Seeds normally contain sufficient food for growth, so that we do not usually think of food as a condition that is essential for germination.

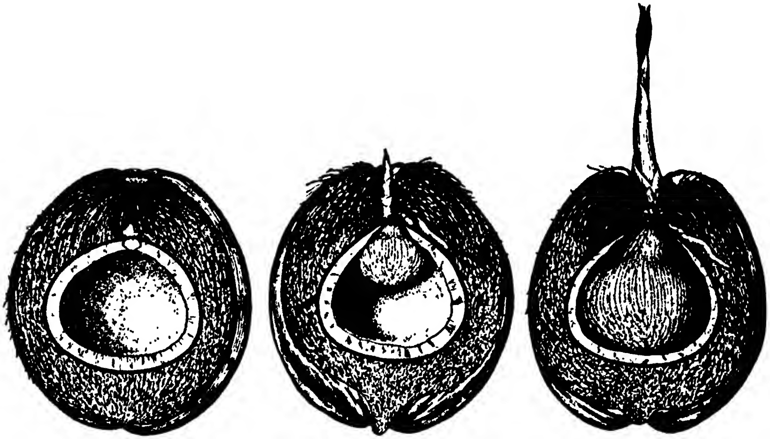


FIG. 389. Successive stages in the germination of coconut

The large central meat is endosperm. In the drawing at the left the embryo is still very small; the cotyledon, which is modified as an absorbing organ, is in the endosperm, while the remainder of the embryo projects up into the husk. In the second drawing the modified cotyledon has enlarged, while the shoot appears through the husk. In the third drawing the cotyledon fills the cavity in the kernel. (× $\frac{2}{15}$)

Active protoplasm consists very largely of water, while the protoplasm of dry seeds contains comparatively little water. A supply of water is therefore very essential to change the protoplasm from the relatively inactive conditions in the dry seed to the active conditions in the young seedling. The amount of water absorbed is frequently considerable, and it is absorbed with great force. During the process the seeds become soft and saturated with water. This absorption of water causes most seeds to swell.

The source of energy in germination is respiration, or, in other words, the oxidation of food material stored in the seed. The amount of energy necessary is considerable, as germination requires that the material stored in the seed be rapidly transformed into tissues. Large quantities of oxygen are therefore necessary, and seeds will not germinate unless there is an abundant supply. For this reason most seeds fail to germinate in poorly aerated soil, as when buried at a great depth or when the air spaces of the soil are filled with water.

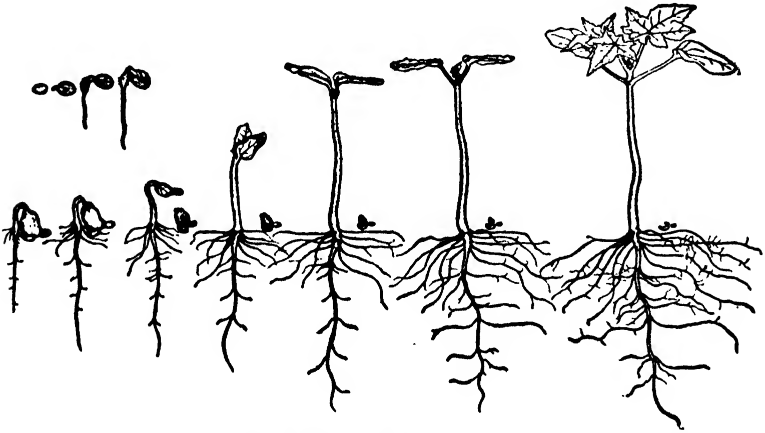


Fig. 390. Successive stages in the germination of castor-oil seed

The cotyledons first act as absorbing organs and later become green foliage leaves. Compare with Fig. 360

Selection of seeds. The value of knowing the hereditary characters that are carried in a seed will be discussed in the next chapter. In selecting the seeds for planting there are certain other points which it is important to take into consideration. Among these are the size and vigor of the plant producing the seed, and the size of the seed itself. Vigorous plants are more likely to produce vigorous offspring than are weak ones; and large seeds are much more likely than small ones to give rise to robust plants. A large seed indicates vigor and abundant food material for the nourishment of the young plant. Care should be taken that seeds are fully matured. Immature seeds often do not germinate; if they do germinate, they often produce weak seedlings. The age of the seed is also important. Many seeds, as we have seen, necessarily undergo a period of rest, and so can be stored for a considerable length of time without injury; but while seeds are apparently inactive, life processes are still going on, even though at a slow rate. If the seeds are stored for too long a time, they begin to lose their vitality; and this process, once started, continues until the seeds reach such a condition that they will no longer germinate.

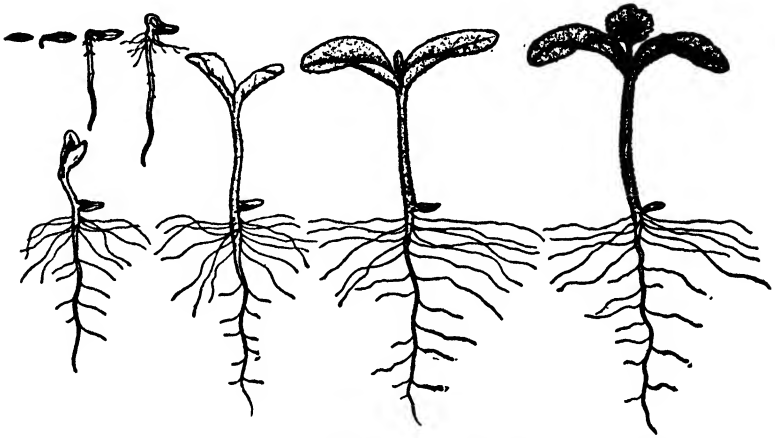


FIG. 391. Successive stages in the germination of squash

Note the peg which catches into the seed coat and holds it while the cotyledons are pulled out. In the seed the cotyledons store food, during germination they supply food to the embryo, and later they serve as green leaves. (× ⅓)

Germination. The principal processes taking place during germination are the transfer of materials and growth. If the reserve food is stored in the cotyledons, it is transferred to the growing plumule and radicle (Fig. 387). When food is stored in the endosperm it is first absorbed by the cotyledons and then conveyed to the regions of growth (Fig. 388). During germination the cotyledon may therefore serve for the storage of food, or, if the food is stored in the endosperm, as an absorbing and transferring organ.

Frequently, as in the grains of the grasses, the cotyledons serve as absorbing organs and do not leave the seeds (Fig. 388). The tip of the cotyledon of the coconut is modified into an absorbing organ which grows so large as to fill the cavity of the nut (Fig. 389).

In some cases in which the seeds contain endosperm (Fig. 390), and in others in which they do not (Fig. 391), the cotyledons are carried up into the air by the growth of the hypocotyl (the part of the seedling between the cotyledon and the root) and function as green leaves. In an intermediate type the cotyledons are carried up into the air by the growing hypocotyl, but shrivel as the reserve food is exhausted and do not function as green leaves (Fig. 392). The orientation of the seedling is frequently due to movements of the cotyledons, which bend in such a way as to push the developing radicle into the ground.

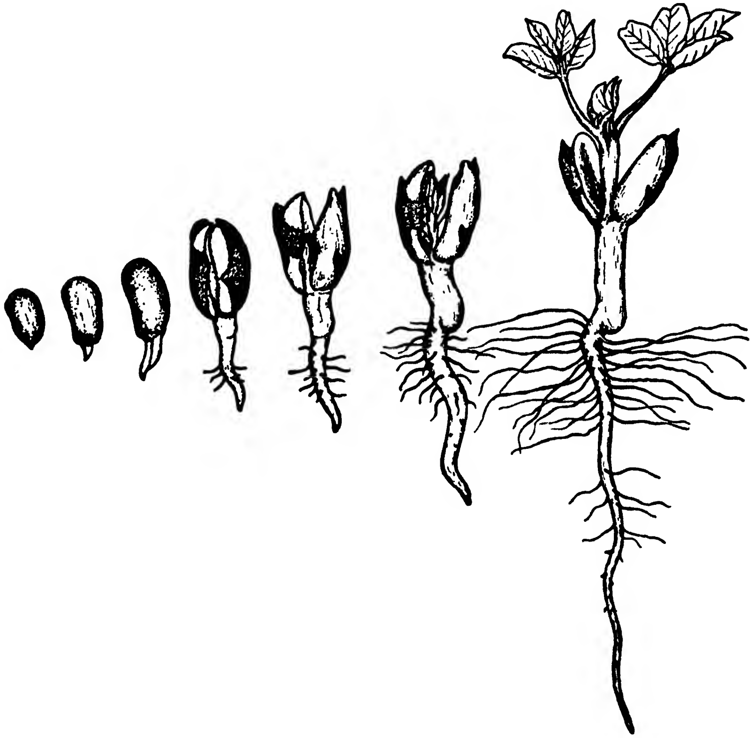


FIG. 392. Stages in the germination of peanut

The cotyledons are carried up into the air; the food is transferred from them to the growing parts of the seedling, while the cotyledons shrivel; they do not become green. (× ½)

CHAPTER XV

HEREDITY

THE NUCLEUS

Since the inheritance of characters is very largely due to the nucleus and the behavior of its constituent parts during fertilization and in the stages which lead to reproduction, some knowledge of the nucleus is essential for an understanding of heredity.

Resting nucleus. The nucleus when not in a state of division is called a resting nucleus. This designation is somewhat unfortunate, as the nucleus of an ordinary cell must be carrying on many activities even though no morphological changes may be evident.

The nucleus (Fig. 393, *A*) is usually rounded, and is surrounded by a membrane known as the *nuclear membrane.* Within this there is a clear substance, the nuclear sap or *karyolymph,* which is not readily stained. Embedded in the karyolymph is a network, or *reticulum.* This is usually said to be composed of *linin* on which another substance, *chromatin,* is distributed. Chromatin is very easily stained, so that it is conspicuous in stained preparations. The nucleus also usually contains one or more rounded bodies, the *nucleoli.* The function of the nucleoli is somewhat obscure, and it is probable that they have various functions in different cells. In general, however, the nucleolus would seem to be a mass of accumulated material which is usually, though not always, utilized in the metabolic processes of the nucleus.

Mitosis. The division of the cell is initiated by the division of the nucleus. In the ordinary method of division a nucleus passes through many stages, and the whole complicated process is known as mitosis. Its chief function seems to be to divide all parts of the chromatin equally between the two daughter nuclei. Mitosis may be considered as consisting of the following stages: *prophase, metaphase, anaphase,* and *telophase.*

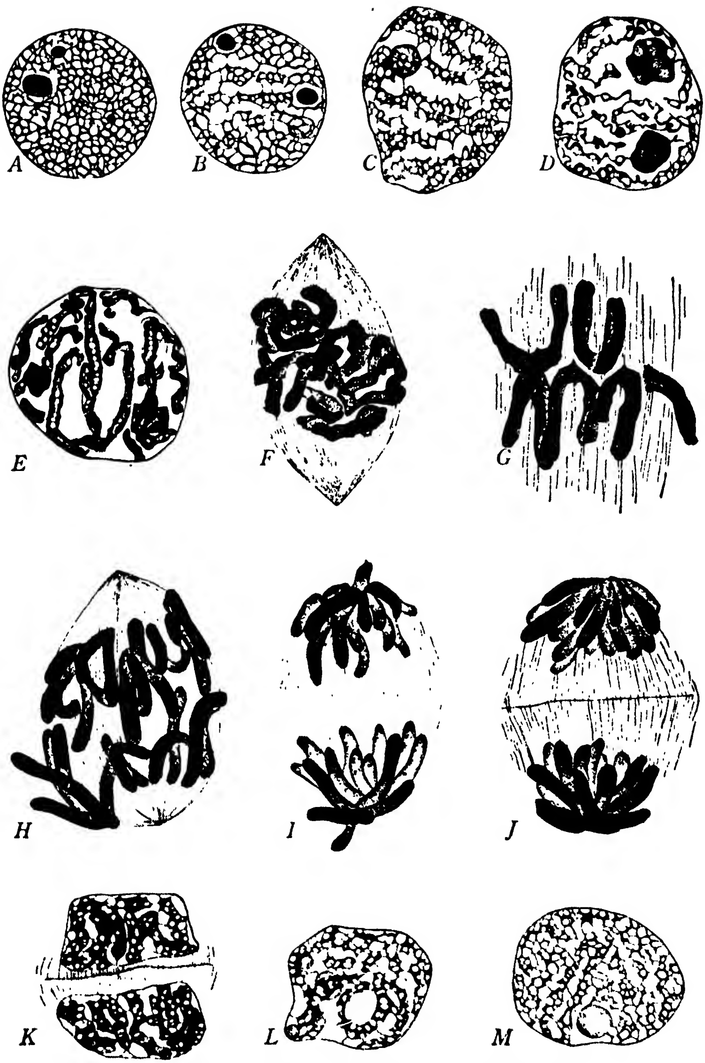


FIG. 393. Successive stages in division and reorganization of nuclei of *Tradescantia*

All except *H* and *I* redrawn after Sharp. (× 1500)

Prophase. In the resting nucleus the chromatin is spread out as a reticulum. It is actually composed of a number of separate units, the *chromosomes.* These are, however, so spread out and so joined by anastomoses with each other that their individuality is obscured.

The initiation of the division of the nucleus is marked by the resolving of the reticulum into distinct chromosomes (Fig. 393). The material of the chromosomes condenses and becomes more or less evenly distributed along the length of the chromosomes. This results in giving them a dense appearance. At this stage they are long, slender, threadlike structures. They undergo shortening and thickening and the different chromosomes come to have very characteristic shapes. In their final form they are most frequently somewhat long and slender. Very early in the prophase each chromosome is seen to be split into two parts, the *chromatids.* These two parts, however, remain together until the next stage of mitosis, that is, until metaphase.

Chromosomes are carriers of hereditary characteristics, and there is very decisive evidence to show that the factors for these characters are arranged lineally in the chromosomes themselves. The splitting of the chromosome lengthwise into two parts divides each of the factors very exactly, and the whole process of mitosis seems to be an arrangement to insure an equal distribution of the hereditary factors to each daughter nucleus. The remaining part of the mitotic process is such as to distribute one chromatid from each chromosome to each of the daughter nuclei. It is owing to this even distribution that the daughter nuclei are alike in hereditary characteristics.

Toward the end of the prophase great changes occur in the nucleus. The nuclear membrane disappears and the whole mass of karyolymph becomes spindle-shaped. When nuclei in this stage are prepared for study by being fixed, sectioned, and stained, the karyolymph has a striated or fibrillar appearance with the fibrils converging toward the poles of the spindles.

In living cells the fibrous appearance is not evident and the spindle appears homogeneous. The spindle is dense enough so that with a needle it can be moved through the cytoplasm. There is doubt as to the meaning of the fibrous structure brought about by fixing and staining, but it seems to be connected with the invisible structure of the spindle.

As the nuclear membrane disappears and does not form part of the daughter nuclei, it cannot be regarded as a permanent cell organ. During the early stages of prophase the nucleolus usually becomes steadily smaller and may disappear altogether, indicating that it constitutes a store of reserve material which is drawn on during the process of division. If the nucleolus persists after the disappearance of the nuclear membrane, it lies free in the cytoplasm and finally disappears. Like the nuclear membrane, therefore, it cannot be considered as a permanent part of the nucleus.

Metaphase. As the spindle forms, the chromosomes quickly become arranged in a single plane at the equator of the spindle, to which they become attached. The stage during which they are in this position is called metaphase (Fig. 393, *G*). By the end of metaphase the chromatids of each chromosome have separated lengthwise to form two daughter chromosomes.

Anaphase. After metaphase one of each pair of daughter chromosomes travels to one pole, and the other chromosome of each pair to the opposite pole (Fig. 393, *H*). The stage during which the daughter chromosomes move from the equatorial region of the spindle toward the poles is known as anaphase.

Telophase. When the chromosomes reach the poles, they collect into a more or less solid-appearing mass. This marks the beginning of telophase (Fig. 393, *I*, *J*). Soon clear droplets of karyolymph appear within the mass of chromosomes and also between the outermost chromosomes and the cytoplasm (Fig. 393, *K*). Where the karyolymph comes in contact with the cytoplasm a nuclear membrane is produced. The formation and enlargement of the spaces containing karyolymph continue (Fig. 393, *L*) until the chromosomes again become scattered in the form of a network typical of the resting stage (Fig. 393, *M*). As the mass of chromosomes becomes more and more spread out by the formation of karyolymph a new nucleolus makes its appearance.

Formation of cell wall. Until very recently the division of the protoplasm was described as being initiated by the formation of small thickenings on the fibers in the equatorial region when the chromosomes become collected at the poles. The spindle fibers gradually spread out until the sides of the spindle reach the sides of the cell wall, and the thickenings were believed to grow until they formed a plate across the original cell dividing it into two (Fig. 394). According to more recent investigators, what actually happens is that minute droplets of liquid appear in the equatorial region of the spindle and that these coalesce to form the so-called plate (Fig. 394). Protoplasmic membranes are then formed by the protoplasm on both sides of the liquid layer, and the cell walls are laid down between the protoplasmic membranes.

Individuality of the chromosomes. The number of chromosomes in a nucleus varies greatly with different species but is constant for the same species. The chromosomes are believed to retain their individuality through the resting stage of the nucleus, and so from one cell generation to the next. In other words, the same chromosomes that pass to a pole in the anaphase of one division reappear during the prophase of the succeeding division. During the organization of a daughter nucleus from a group of chromosomes the chromosomes become connected by anastomoses. When the chromosomes reappear in the succeeding prophase these anastomoses break down and the chromosomes are separate. Indeed, where cell divisions follow each other in rapid succession the spreading out of the chromatin during the resting stage may not go far enough to obscure the identity of the individual chromosomes.

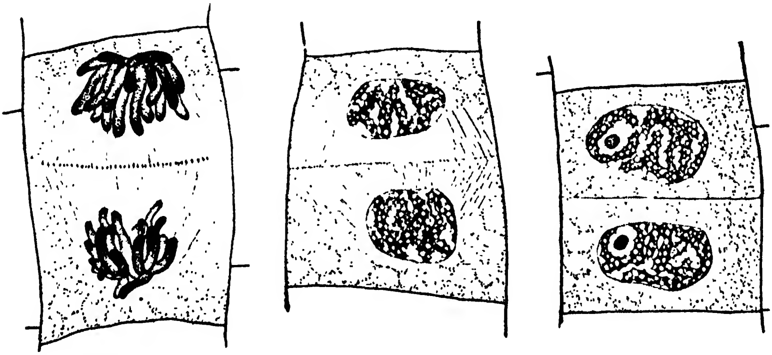


FIG. 394. Successive stages in the formation of a cross wall between two daughter cells in *Tradescantia* root tip. (× 1300)

In following the process of division we have seen that the nuclear membrane and the nucleoli disappear during division and are formed anew during the organization of the daughter nuclei. The chromosomes persist from one cell generation to the next. For this and other reasons, to be mentioned later, they are generally regarded as the most important constituents of the nucleus and as the site of the mechanism or factors which determine the hereditary characteristics of an organism.

Chromosomes and fertilization. During the process of fertilization the male nucleus and the egg nucleus come together and the sides that meet become flattened against each other. The parts of the two nuclear membranes that are in contact disappear, and thus the contents of the two nuclei come to be enclosed by a single nuclear membrane, a part of which comes from the male nucleus and a part from the egg nucleus. In this way the chromosomes which were in the male nucleus are added to those which were in the egg nucleus. The fertilized egg thus contains the chromosomes of both the egg nucleus and the male nucleus, or, usually, double the number of chromosomes that were in either of the fusing nuclei.

When the fertilized egg nucleus divides, every chromosome splits into two, and one of each pair of the resulting chromosomes goes to each daughter nucleus. In this way each daughter nucleus contains the same number of chromosomes as the nucleus of the fertilized egg. The chromosomes divide in the same manner in the second and all subsequent nuclear divisions in the vegetative parts of the organism, and so the same number of chromosomes are distributed to every cell in these parts.

Reduction of the number of chromosomes. If the same number of chromosomes as are found in the vegetative nuclei went into the egg and sperm nuclei, the fertilized egg of each generation would contain twice as many chromosomes as the nuclei of the preceding generation. This result is prevented by the presence of two successive divisions in the life cycle in which the number of chromosomes is reduced to half that found in the ordinary vegetative nuclei. In flowering plants this reduction takes place before the formation of pollen grains, and also before the development of the embryo sac.

Each anther produces a number of cells known as pollen mother cells. By two successive divisions each pollen mother cell gives rise to four pollen grains. The reduction in the number of chromosomes takes place in the first two divisions of the pollen mother cell, so that the nuclei of the pollen grains, and consequently the male nuclei, contain half the number of chromosomes found in ordinary vegetative nuclei.

The formation of the embryo sac is preceded by the development of a single rather conspicuous cell called a spore mother cell. This gives rise, by two successive divisions, to four cells which are known as *spores*. The reduction in the number of chromosomes takes place during the divisions of the spore mother cell to form spores. Typically, three of the spores degenerate and disappear, while the other develops and produces the embryo sac. The nuclei of the embryo sac, including the nucleus of the egg, thus resemble the male nuclei in containing half the number of chromosomes found in the ordinary vegetative nuclei. The union of the male nucleus with the female nucleus gives the fertilized egg the same number of chromosomes as were in the fertilized egg of the preceding generation. Thus the same number of chromosomes is preserved from generation to generation. The number of chromosomes found in the egg or sperm nucleus is called *haploid*, while the number which is present in the fertilized egg and in the vegetative parts of the organism is *diploid*.

Homologous chromosomes. We have already noted that the chromosomes carry hereditary characteristics and that in a chromosome the factors responsible for these characteristics are arranged lineally. The different chromosomes of a plant are not alike but carry different hereditary characteristics. In fact, in the set of chromosomes received from one parent, each chromosome, except in exceptional cases to be mentioned later, is different from every other chromosome of the set and carries different hereditary factors. The sets received from the two parents are similar, however, and each chromosome of a set from one parent is more or less similar to and homologous with a corresponding chromosome received from the other parent.

Meiosis. The divisions during which the number of chromosomes are reduced are known as the reducing or meiotic divisions, and the process of reduction as *meiosis*. We have seen that in the prophase of an ordinary division each chromosome splits into two chromatids. It has therefore a double structure. During the prophase of the first meiotic divisions, each chromosome splits into two chromatids as in an ordinary division. The feature which characterizes the prophase of this division is that the homologous chromosomes approach each other and come to lie side by side (Fig. 395). The union between these two chromosomes comes to be very intimate. The two chromosomes may be joined together in one or more places. The stage during which the homologous chromosomes come into this intimate union is known as *synapsis*. The union of the two homologous chromosomes is so intimate that the combination is known as a bivalent chromosome, the term "bivalent" signifying that the chromosome is composed of two homologous chromosomes. As each of the two chromosomes which compose the bivalent chromosome is split into two chromatids, the bivalent chromosome is really a quadruple structure and is called a tetrad chromosome (Fig. 396). After the formation of the tetrad chromosomes, the nucleus has only half the number of chromosomes that are found in ordinary vegetative cells. The subsequent events in this and the next division distribute one of the chromatids of the tetrad to each of four cells.

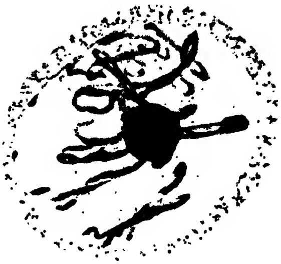


Fig. 395. Prophase of first meiotic division in sugar cane showing chromosomes lying side by side

After Santos

At metaphase each of the tetrad chromosomes is separated longitudinally into two daughter chromosomes which pass to opposite poles. Each of these chromosomes is, however, already split into two chromatids. At metaphase of the second of the reduction divisions, these chromatids are separated from each other. We can now see why there are two reducing divisions. This is connected with the fact that the chromosomes which are formed in the prophase of the first meiotic division are quadruple and that it takes two divisions to divide them up into their constituent chromatids. At the end of the second reduction division not only has each chromosome been reduced to a single chromatid but the total number of chromosomes is also haploid.

The dividing of a tetrad chromosome in the first reduction division may be in such a plane as to separate two homologous chromosomes from each other, or each of the homologous chromosomes may be split in two. In this case each of the two daughter chromosomes which move to the poles at anaphase will consist of a chromatid from each of the homologous chromosomes which united to form the tetrad chromosome. At metaphase some of the chromosomes may behave in one of the ways described above and others in the other way. In any case the result is the same at the end of the second reduction division.

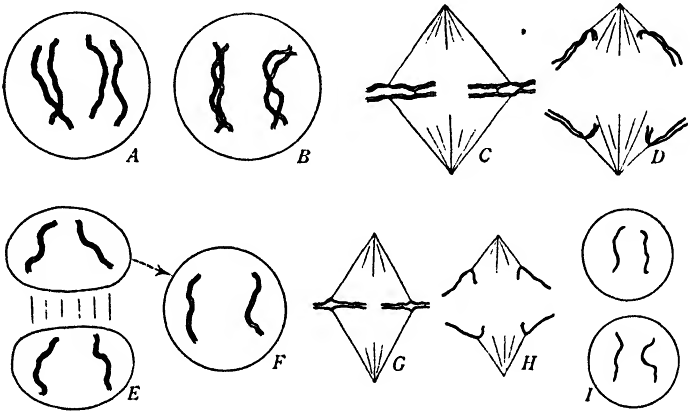


FIG. 396. Diagram of meiotic divisions

A, a nucleus with two pairs of homologous chromosomes; each chromosome is split into two chromatids and homologous chromosomes are approaching each other. *B*, the members of each pair of homologous chromosomes have united to form a tetrad chromosome; as there were two pairs of chromosomes in *A*, there are two tetrad chromosomes in *B*. *C*, metaphase of first meiotic division; homologous chromosomes are being separated from each other. *D*, anaphase of first meiotic division; single chromosomes, each split into two chromatids, are moving toward the poles. *E*, two nuclei formed as the result of first meiotic divison; each contains two chromosomes, each split into two chromatids. *F*, one of the daughter nuclei. *G*, metaphase of the second meiotic division; two chromatids are being separated from each other. *H*, single chromatids, now chromosomes, are moving toward the poles. *I*, two nuclei resulting from the second meiotic division; each has a single chromosome consisting of a single chromatid

While a set of chromosomes in the egg nucleus of one plant is believed to carry a set of hereditary factors very similar to the set in any egg or male nucleus of the same species, these sets of factors are not necessarily identical, as different individuals within the same species frequently show different hereditary characteristics. This subject will be considered at some length in the section on heredity, where it will be shown that the behavior of the chromosomes is intimately connected with the laws of heredity.

HEREDITY

The fact that, in general, offspring tend to resemble their parents has been known from early times. The modern conception of the definite laws of heredity, however, is of comparatively recent date and may be said to have begun with Mendel. In 1865, after eight years of investigation, Mendel read the results of his work before the Natural History Society of Brünn, and the following year he published them in the transactions of that society. Unfortunately his results were neglected until independent investigations by three botanists led to their rediscovery in 1900. It was then found that Mendel had discovered fundamental laws of heredity. The type of inheritance described by him is now known as *Mendelism.*

Mendelism

Color inheritance in the four-o'clock. The subject of inheritance can best be introduced by means of a few examples. If red-flowered four-o'clock plants are crossed with white-flowered ones, the offspring will have pink flowers. If one of these plants with pink flowers is self-pollinated, or if pink-flowered plants are cross-pollinated, their offspring will consist of red-flowered, pink-flowered, and white-flowered plants in the proportion of one red, two pink, and one white. If now the red-flowered plants are self-fertilized, all their offspring will have red flowers, and successive generations will continue to have red flowers for as many generations as they are self-fertilized. In the same way, if the white-flowered plants are self-fertilized, their offspring will have white flowers. When, however, pink-flowered plants are self-fertilized, they will, like their pink-flowered parents, again produce red-flowered, pink-flowered, and white-flowered plants in the ratio of one red, two pink, and one white. The inheritance of the flower color in this plant, and its explanation in terms of *factors* and

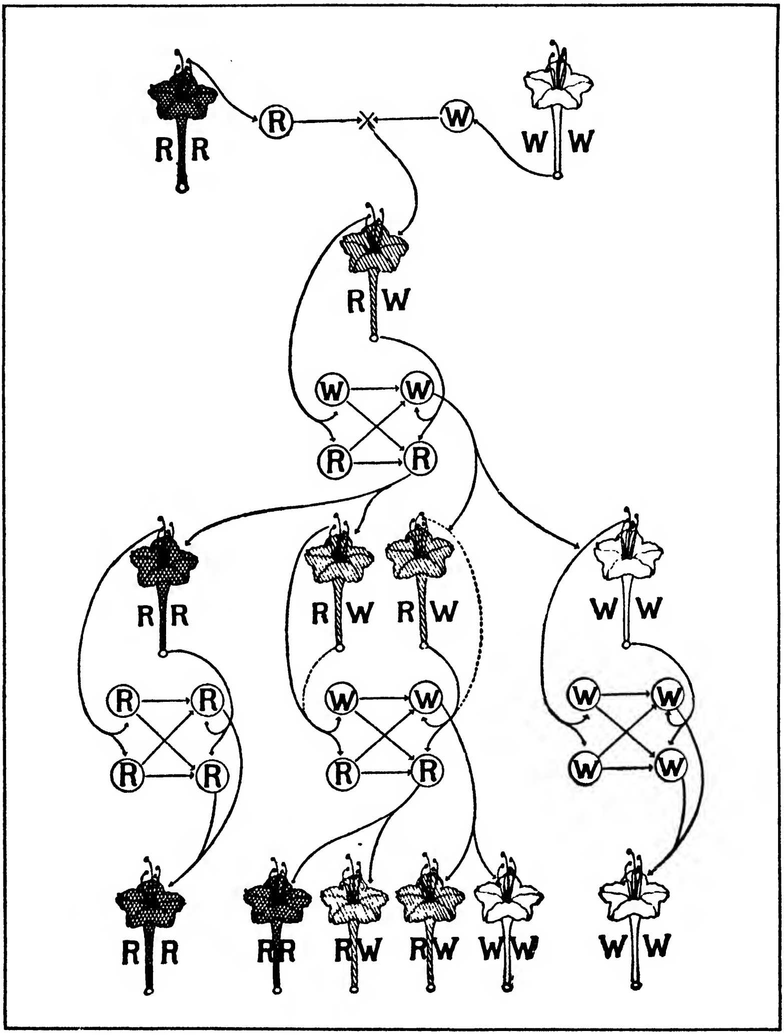


FIG. 397. Diagrammatic representation of inheritance of flower color in four-o'clock

The flowers represent individuals: cross-hatching, red; single hatching, pink; unshaded, white. The letter R represents a factor for red; W, a factor for white. Rings signify gametes; straight lines represent union of sperm and egg; curved lines, the production of offspring chromosomes, is shown in Fig. 397. The flowers represent plants; R, a chromosome carrying a factor for red; W, a chromosome with a factor for white. Circles represent *gametes* (sexual cells).

The explanation of color inheritance in the four-o'clock is as follows: Two chromosomes in a red-flowered plant have a factor for red. During the reduction division these segregate so that the gametes possess only a single chromosome with a factor for red. Likewise, a white-flowered plant has two factors for white, while a gamete produced by a white-flowered plant carries only one such factor (line 1, Fig. 397).

The hybrid (known as the F_1, or first filial, generation) is therefore produced by the union of a gamete with a chromosome carrying a factor for red and a gamete having a chromosome with a factor for white. The result is that the hybrid possesses both a factor for red and one for white, and is pink-flowered (line 2, Fig. 397). When this individual gives rise to gametes, these will be of two kinds, some with a chromosome bearing a factor for red and others with a chromosome bearing a factor for white. Just as the chromosome carrying the factor for red and that with the factor for white came together in the fertilized egg, so they again separate before the formation of gametes. The union of the gametes produced by the F_1 hybrids gives rise to the generation called F_2, which is shown in Fig. 397. If a male nucleus with the factor for red fertilizes an egg with the factor for red, the result will be a plant which has two factors for red in all its vegetative cells and which will produce red flowers. Likewise, if a male nucleus with a factor for white fertilizes an egg with a factor for white, the fertilized egg will have two factors for white and the plant will produce white flowers. When, however, a male nucleus with a factor for white fertilizes an egg which has a factor for red, or vice versa, the fertilized egg has a single factor for white and a single factor for red, and the resulting plant will have pink flowers. When the F_1 hybrid gives rise to sexual nuclei, there will be, on the average, an equal number of egg nuclei with the factor for red and egg nuclei with the factor for white. Likewise there will be an equal number of pollen grains with the factor for red and pollen grains with the factor for white. The two kinds of male nuclei produced will, according to chance, fertilize an equal number of eggs. Moreover, each kind of male nucleus will tend to fertilize an equal number of eggs with the factor for red and eggs with the factor for white. The male nuclei with the factor for red will then fertilize eggs in the ratio of one with the factor for red to one with the factor for white, so that there will be one plant with red flowers to one with pink flowers. In a similar way, the male nuclei with the factor for white will give rise to one plant with pink flowers to one plant with white flowers. Thus we get plants in the ratio of one plant with red flowers, two with pink, and one with white (Fig. 397).

Purity of gametes. Inheritance of color in the four-o'clock illustrates one of the fundamental principles of Mendelian inheritance, that is, *purity of gametes.* The fusion of two gametes with alternative characters, such as red and white, results in a hybrid the body cells of which will contain the factors for both characters. When, however, this plant produces gametes, the factors for these two characters will separate, and one of them will be found in one gamete and the other in another gamete. One gamete will thus contain only one of two such alternative characters. In other words, a gamete of a four-o'clock can contain either a factor for red or a factor for white, but not both. In this way the alternative characters are segregated when gametes are formed, so that no gamete is a hybrid so far as a single pair of characters is concerned.

Segregation and chromosomes. The explanation of the segregation of factors and the purity of gametes is found in the chromosomes. In the chromosomes are located the factors responsible for Mendelian inheritance. Each gamete contains a complete set of chromosomes. When a male nucleus fuses with the egg nucleus, the fertilized nucleus has two sets of chromosomes. Naturally there are two sets of hereditary factors, one brought in from the male plant by the male nucleus and the other coming from the female plant through the egg nucleus. In the case of the four-o'clock, when red-flowered and white-flowered plants are crossed, a chromosome from the red-flowered parent carries a factor for red and the corresponding or homologous chromosome from the other parent carries a factor for white. At each mitosis a daughter chromosome from each chromosome of the fertilized egg is distributed to each daughter cell. Each cell of the plant, including those of the flowers, has therefore a chromosome with a factor for red and a chromosome with a factor for white. The production of sexual cells is preceded by the reduction divisions. During these the number of chromosomes is, as we have seen, reduced, and each of the four cells resulting from the two reduction divisions will have only one of two homologous chromosomes. In the case cited, it will have either a chromosome with a factor for red or a chromosome with a factor for white but not both. For this reason the gametes are pure in regard to a single factor.

Definition of terms. In discussing heredity there are a few technical terms which are very convenient and which are used in even the simplest discussions of the subject. A few of these are here defined.

A *gamete* is a cell that fuses in sexual reproduction. A *zygote* is a cell formed as the result of sexual fusion. Two alternative characters, such as tallness and dwarfness, are known as *allelomorphs*. An individual is said to be *homozygous* for a certain character when it contains two factors for that character and does not contain the factor for the other member of the pair of allelomorphs. An individual is said to be *heterozygous* when it contains factors for both members of a pair of allelomorphs. When two plants are crossed, the parent plants are known as the P_1 generation, and the resulting offspring as the F_1 generation; when this generation is self-fertilized or interbred, the offspring compose the F_2 generation; the subsequent generation is known as the F_3 generation; etc.

Dominance. Mendel crossed tall and dwarf varieties of garden peas and found that their offspring in the first generation were all tall. These may be called tall hybrids, as they were produced by crossing tall and dwarf varieties. When these tall hybrids were self-fertilized, they gave rise to tall and dwarf plants in the ratio of three tall ones to one dwarf. When the resulting dwarf plants were self-pollinated, they always produced dwarf offspring. One third of the tall ones contained two factors for tallness and none for dwarfness, and when self-fertilized always gave rise to tall offspring only, while the other two thirds, which were tall hybrids, produced dwarf and tall, as did their hybrid parents, in the ratio of one dwarf to three tall. These tall plants, like those of the preceding generation, consisted of one third which had no factor for dwarfness and always gave rise to tall plants when self-pollinated, and two thirds which were tall hybrids and again repeated the ratio of three tall to one dwarf. This relation is shown in Fig. 398. The inheritance of the factors for tallness and dwarfness after the crossing of tall and dwarf plants is shown by the letters under the words describing the heights of the plants. T represents tallness; D, dwarfness; and (D), dwarfness which is dominated by tallness.

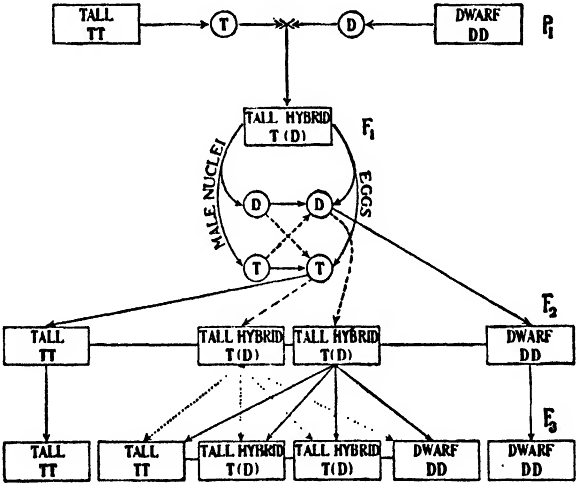


Fig. 398. Diagram showing inheritance of tall and dwarf characters in peas; also inheritance of factors for tallness T and dwarfness D. (D) signifies dwarfness dominated by tallness

In the case just discussed, when tall plants were crossed with dwarf ones their offspring were all tall. If plants with two opposite characters are crossed and their offspring show one of the characters and no influence of the other, then the character which appears in the offspring is said to dominate, or to be a *dominant* character. A character which does not appear is said to recede, or to be a *recessive* character. In this case tallness is a dominant character as compared with dwarfness. Dominance, like purity of gametes, is an important Mendelian principle. In the case of the four-o'clock plants the red color of the flowers is not nearly so dominant as is tallness in peas. The red color of the four-o'clock is said to be incompletely dominant.

In different cases there may be various degrees of dominance. In some plants flower color may be just as dominant as tallness in peas, while in other plants length may be only partially dominant. Thus the fact that a character is dominant in one species does not necessarily imply that it is dominant in other species. Such facts can be determined only by observation.

On examining Fig. 398 we find that the factors for tallness and dwarfness are inherited in exactly the same way as the factors for color in four-o'clock plants. When a pure strain of tall peas is crossed with a dwarf one, the plants of the first hybrid generation contain a factor for tallness and also a factor for dwarfness, even though the factor for dwarfness is recessive. These plants, if self-pollinated, will produce three kinds of plants, even though on superficial examination there would appear to be only two. The three kinds are produced in a ratio of one which has two factors for tallness and none for dwarfness, and so can produce only tall offspring; two which contain both the factor for tallness and the factor for dwarfness, and so can produce both tall and dwarf offspring; and one which contains two factors for dwarfness and none for tallness, and so can produce only dwarf offspring. The plants which contain both the factor for tallness and the factor for dwarfness will be like their hybrid parents in hereditary height factors, and so will naturally give rise to the same kinds of plants as did their parents, and in the same proportion.

In writing the abbreviations of characters it is very convenient as well as customary to represent the dominant character by a capital letter, as *T* for tallness, and the recessive character by the same letter not written as a capital. Thus, when tallness is dominant over dwarfness, dwarfness may be indicated by *t*.

Inheritance of two pairs of characters. When we observe any organism we see that it is a morphological and physiological unit. From the standpoint of inheritance it is, however, made up of a number of hereditary units or characters, which most often appear to be inherited independently of each other. The examples of inheritance which we have considered demonstrate very clearly the segregation of characters and the purity of gametes, while the inheritance of height in peas is a good example of dominance. The independence of characters can be emphasized by a consideration of the inheritance of two pairs of characters which Mendel studied in garden peas.

In peas round seed is dominant over wrinkled seed, and yellow seed over green seed. When, therefore, we cross a plant having round yellow seed with one having wrinkled green seed, the F_1 generation will have round yellow seed. If these hybrids are self-fertilized, they will give rise to the following kinds of plants in the following ratio: nine with round yellow seed, three with round green seed, three with wrinkled yellow seed, one with wrinkled green seed. This relationship is shown in Fig. 399, in which the small squares represent individuals, while circles represent gametes. R stands for a factor for round; r, for wrinkled; Y, for yellow; and y, for green.

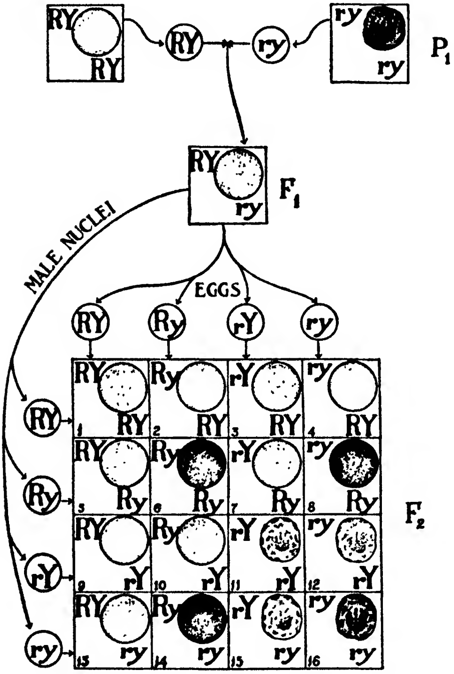


FIG. 399. Diagram showing inheritance of seed characters in garden peas

Squares represent individuals; circles containing letters are gametes; letters represent factors as follows: R, round; r, wrinkled; Y, yellow; y, green

From the diagram it will be seen that the F_1 generation contains a factor for round, one for wrinkled, one for yellow, and one for green. When this plant forms gametes, both the male and the female gametes will show four different combinations of factors: namely, round and yellow, round and green, wrinkled and yellow, and wrinkled and green. A male nucleus with the factors for round and yellow can fertilize any of the four kinds of eggs, and, according to chance, will fertilize the different kinds in equal numbers. Likewise the three other kinds of male nuclei will fertilize all four kinds of eggs in equal numbers. The different combinations produced are shown in squares in the lower part of the diagram. Such a set of squares may be very simply constructed by writing the factors for one of the kinds of eggs in each square of the first vertical row of squares, and the factors for each of the other kinds of eggs in a separate vertical row of squares. The characters for male nuclei should be similarly written in horizontal rows. If we examine the squares in the lower part of the diagram, we shall see that there are nine which contain both R and Y, and so represent plants with round yellow seed; three which contain R but not Y, and so represent plants with round green seed; three which contain Y but not R, and so represent plants with wrinkled yellow seed; and one square which contains neither R nor Y, and so represents a plant with wrinkled green seed. The last-mentioned square is the only one of the sixteen which represents a plant that is pure for both recessive characters. Likewise, there is only one of the sixteen squares which represents a plant that is pure for both dominant characters.

A line drawn diagonally from the upper left-hand corner to the lower right-hand corner of the large square in the lower part of Fig. 399 passes through four small squares, each of which represents a different kind of individual that is homozygous for one of each of the two pairs of characters. Similarly, a line drawn from the lower left-hand corner to the upper right-hand corner of the large square passes through four small squares, each of which is heterozygous for both pairs of characters.

The F_2 generation of a cross between peas having round yellow seed and peas having wrinkled green seed shows very clearly that in this case the pairs of characters are independent of each other. In other words, round and yellow, and likewise wrinkled and green, are inherited independently of each other.

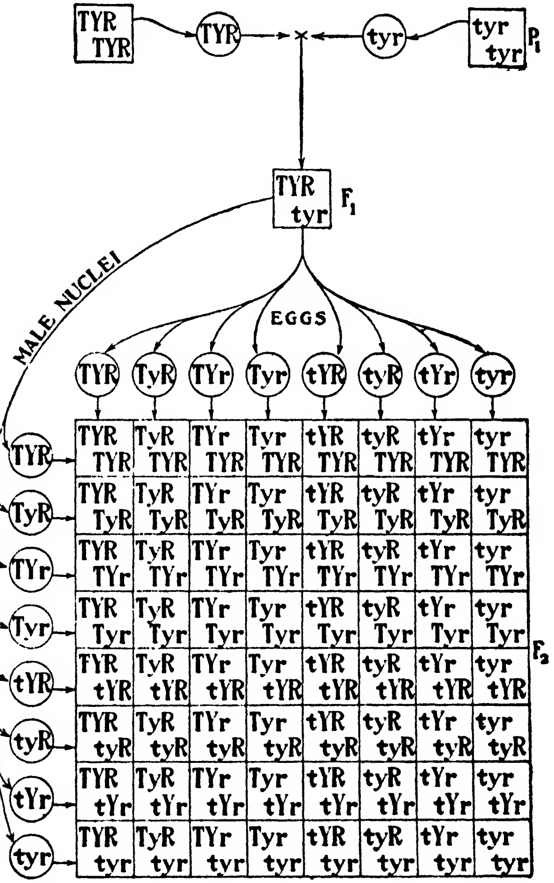
Linkage. The number of different chromosomes in an organism is usually not very great; on the other hand, the organism has a large number of characters. It should follow from this that one chromosome would carry several or many different factors. Moreover, factors which are in the same chromosome should be linked together in inheritance. This reasoning is borne out by the fact that many characters are linked together in inheritance. In the Chinese primrose the factors for red stigma, red flower color, long style, dark stem, and light corolla tube are linked together. In garden peas the factor for round seed as opposed to wrinkled seed and the factor for tendriled as opposed to non-tendriled leaves go together. We may conclude, therefore, that factors in the same chromosome are linked together, while those in different chromosomes are independent.

Cross-over. During the prophase of the first reduction division, two homologous chromosomes come to lie very close together, are often more or less twisted around each other, and, in places, are actually joined together. At this stage each chromosome is split into two chromatids, and so chromatids from homologous chromosomes may be in very intimate union. It sometimes happens that, owing to this intimate connection, chromatids of homologous chromosomes exchange parts before separating at metaphase. The net result is as though each chromatid had been broken across and when the break was repaired the union was not between parts of the same chromatids but between parts of different but homologous chromatids. It appears that in such cases the union of two homologous chromatids has been so close at the point where the exchange occurs that separation takes place not between the original chromatids but across them, so that afterwards each chromatid is made up of parts of two homologous chromatids. Such exchanges between homologous chromatids are known as *cross-overs*. It has been found that different parts of a chromosome carry different factors, and so cross-overs afford a means for the interchange of factors which are linked together.

Trihybrids. In the consideration of the inheritance of two pairs of characters we have seen that sixteen combinations are involved in the F_2 generation. These include plants of four different appearances and nine different germinal compositions. When three pairs of characters are considered, sixty-four individuals are involved in the F_2 generation. These include plants of eight different appearances and twenty-seven different germinal compositions. Only one of the sixty-four contains only dominant factors, and, likewise, only one contains only recessive characters.

The inheritance of three pairs of characters may be illustrated by garden peas. In these plants we have seen that tallness is dominant over dwarfness, yellow seed is dominant over green seed, and round seed is dominant over wrinkled seed. If tall individuals with yellow round seed are crossed with dwarf ones with green wrinkled seed, the offspring in the F_1 generation will contain factors for tallness, dwarfness, yellow, green, round, and wrinkled; but all the individuals will be tall with yellow round seeds, as these characters are dominant.

When the F_1 generation forms gametes, these are of eight kinds, and the fusing of eight kinds of eggs with eight kinds of male nuclei gives rise to sixty-four combinations. These relationships are shown in Fig. 400, in which T represents tall; t, dwarf; Y, yellow; y, green; R, round; and r, wrinkled.



	TYR	TyR	TYr	Tyr	tYR	tyR	tYr	tyr
TYR	TYR TYR	TyR TYR	TYr TYR	Tyr TYR	tYR TYR	tyR TYR	tYr TYR	tyr TYR
TyR	TYR TyR	TyR TyR	TYr TyR	Tyr TyR	tYR TyR	tyR TyR	tYr TyR	tyr TyR
TYr	TYR TYr	TyR TYr	TYr TYr	Tyr TYr	tYR TYr	tyR TYr	tYr TYr	tyr TYr
Tyr	TYR Tyr	TyR Tyr	TYr Tyr	Tyr Tyr	tYR Tyr	tyR Tyr	tYr Tyr	tyr Tyr
tYR	TYR tYR	TyR tYR	TYr tYR	Tyr tYR	tYR tYR	tyR tYR	tYr tYR	tyr tYR
tyR	TYR tyR	TyR tyR	TYr tyR	Tyr tyR	tYR tyR	tyR tyR	tYr tyR	tyr tyR
tYr	TYR tYr	TyR tYr	TYr tYr	Tyr tYr	tYR tYr	tyR tYr	tYr tYr	tyr tYr
tyr	TYR tyr	TyR tyr	TYr tyr	Tyr tyr	tYR tyr	tyR tyr	tYr tyr	tyr tyr

Fig. 400. Diagram showing inheritance of three pairs of characters in garden peas: tallness, T, dominant over dwarfness, t; yellow seed, Y, dominant over green seed, y; round seed, R, dominant over wrinkled seed, r

Complementary factors. In all the cases that we have so far considered, a single factor is responsible for the production of a character; but in some cases more than one factor is necessary.

This may be illustrated by the case of two strains of white-grained corn which, when crossed, will give all red grains in the F_1 generation. In the F_2 generation there will be nine red to seven white. This ratio suggests at once that here is a case of the inheritance of two factors. In such a case nine out of sixteen individuals have both dominants of two pairs of allelomorphs.

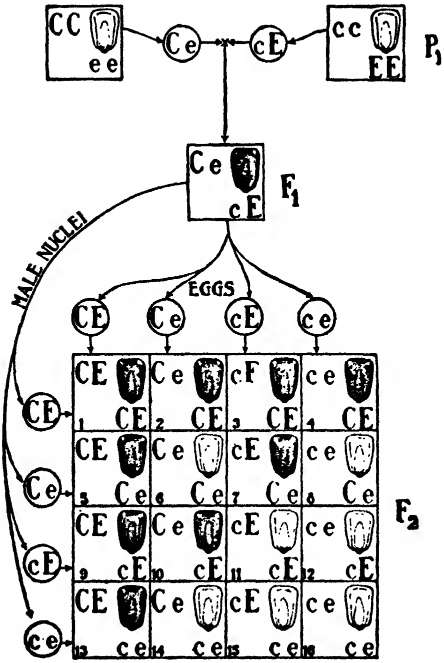


Fig. 401. Diagram of inheritance of complementary factors producing a red color in corn

The complementary factors are dominant and are represented by C and E, while their absence is shown by c and e respectively. Each parent has only one of the complementary factors and is white, while the F_1 hybrid has both factors and is red. The red color in the grain is indicated by stippling

Two factors were necessary to produce the red color, and one of these was present in one of the strains and the other in the other strain. When these two strains were crossed, all the individuals in the F_1 generation contained both factors and so were red. In the F_2 generation nine of the sixteen individuals contained both factors that were necessary for color and so were red, six contained one or the other of the two factors and were white, while one did not contain either of the two factors and so was white. Two factors both of which are necessary for the production of a single character are known as complementary factors.

The inheritance of the factors in the above case is shown in Fig. 401, in which one of the necessary factors is represented as C and its absence as c, while the other is represented as E and its absence as e.

Many pigments in plants are produced by the action of *enzymes* on a colorless substance known as *chromogen.* What may be the explanation of the above case of inheritance in corn is that one of the strains of white-grained corn contained a factor for chromogen and the other a factor for an enzyme capable of acting on the chromogen and producing red. When these two strains were crossed, the resulting plants contained both chromogen and enzyme, and so the grains were red.

A consideration of complementary factors shows that more than one factor may be necessary to produce a given character, and it is probable that any character is the result of several or many factors. When the inheritance of a pair of contrasting characters appears to be due to a single pair of factors, this does not mean that only one factor is necessary for the production of a character, but simply that a difference between two factors of a pair results in the appearance of a pair of contrasting characters. In the case of the inheritance of red color in corn, illustrated in Fig. 401, the color is due to at least two factors. However, if we were to cross the individuals represented by squares 1 and 6 in the lower part of the diagram, red would appear to be a simple Mendelian dominant, conditioned by a single factor, as the two individuals differ from each other only in the factors E and e. Not only is one character the result of the interaction of many factors, but one factor may influence more than one character.

Cumulative factors. Some plants contain more than one pair of factors which produce similar results. Such factors are known as cumulative factors. These may be illustrated by certain strains of wheat. In breeding experiments a strain of wheat with white kernels was crossed with one with red kernels, and the individuals of the F_1 generation were intermediate in color. In the F_2 generation there were fifteen red to one white. Moreover, the red individuals were represented by four shades of red. The explanation of the results is that the red strain contained two pairs of factors for the production of red, that the different factors were cumulative in their action, and that all four factors were necessary for the production of the depth of color shown by the parent red strain. If A stands for a factor of one pair and B for a factor of the other pair, then the red strain may be represented by AABB, and the white strain by aabb. When these two strains were crossed, the F_1 generation contained the factors AaBb. The individuals of this generation thus contained only half as many factors for red as the parent red strain, and their color was intermediate between that of the red and the white strain. When this F_1 generation formed gametes, they were of four kinds, AB, Ab, aB, and ab. Therefore the F_2 generation should show the sixteen combinations characteristic of dihybrids. Fig. 402 shows the results. An examination of the squares in the lower part of the diagram shows that only one out of sixteen does not contain either A or B. This individual has only recessive characters and is white, while the other fifteen are red. Only one, however, contains four factors for red, and this is the only one with as deep a color as the original red strain. Six individuals contain two factors for red, or exactly half the number in the original red strain. The number of factors for red (and so the depth of color) is indicated by the number of the letters R shown in the grains in the squares.

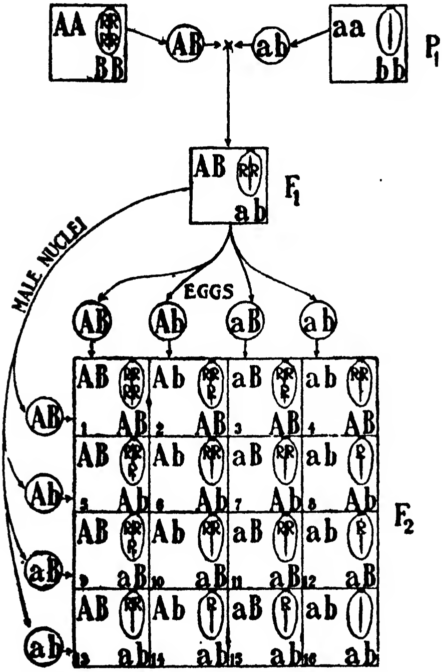


FIG. 402. Diagram representing inheritance of two pairs of cumulative factors, AA and BB, which produce a red color in wheat

The absence of A and B is represented by a and b respectively. Squares represent individuals; circles, gametes. The number of factors for red, and consequently the degree of redness, is shown by the number of the letters R in the wheat grains

Another set of experiments with wheat is even more interesting in connection with cumulative factors. A different red strain was crossed with a white strain, and the individuals of the F_1 generation were again intermediate in color. In the F_2 generation there were sixty-three reds of various shades to one white. In this case the red strain appeared to contain three pairs of factors for red, all of which seemed to produce about the same degree of color and all of which were necessary to produce the depth of color shown by this strain. The proportion of sixty-three red to one white is evidently a trihybrid ratio. In trihybrid ratios there is only one out of sixty-four in the F_2 generation which is purely recessive; so, if the red strain contained three pairs of factors for red, the F_2 generation of a cross between this red and a white should produce only one out of sixty-four individuals without a factor for red. Likewise, there would be only one out of sixty-four which would have six factors for red and which would be as dark as the red strain. In all there were six degrees of redness.

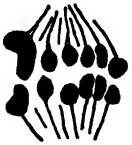


Fig. 403. Meiotic division in *Lychnis alba*

The pair of chromosomes on the left are the sex chromosomes. The one which is above and larger is the female, while the one which is somewhat smaller and below is the male. After Blackburn

In some cases crosses are made in which offspring intermediate in characters appear to breed more or less true to the type of the F_1 generation. It is interesting to consider these cases in connection with cumulative factors. If there were six pairs of cumulative factors, then in the F_2 generation each of the original types would be represented by only one individual out of 4096. The F_1 generation would be intermediate in characters between the two parent forms, and in subsequent generations it would be very rare to find an individual like either of the parent types; unless very large numbers of individuals were reared, such types might altogether fail to appear. The hybrid would then seem to breed more or less true to the hybrid type.

Inheritance of sex. In many animals and quite a number of dioecious plants, the inheritance of sex has been found to be connected with chromosomes (Fig. 403). In *Elodea*, for example, the inheritance of sex is connected with a pair of chromosomes called sex chromosomes. In female plants there are two large sex chromosomes which are spoken of as X chromosomes. In male plants the pair of sex chromosomes consists of a large X chromosome and a small chromosome known as a Y chromosome. The female is homozygous and has two X chromosomes, while the male is heterozygous and has an X and a Y chromosome. As both of the sex chromosomes in the female are X chromosomes, all eggs are alike and contain an X chromosome. The male nuclei, on the other hand, are of two kinds, one with an X chromosome and one with a Y chromosome. When an egg is fertilized by a male nucleus with an X chromosome, a female plant results. When the egg unites with a male nucleus having a Y chromosome, a male plant is produced. Under natural conditions there should be the same number of pollen grains with X chromosomes and pollen grains with Y chromosomes. Random pollination should result, as is the case, in an approximately equal number of female and male plants.

Application of Mendelism. The laws of inheritance known as Mendelism were first discovered in plants. Afterward they were found equally applicable to animals, as well as to human beings. The value of definite laws which can be applied to animal and plant breeding can hardly be overestimated, and human society seems certain to be profoundly influenced by the application to itself of these same laws.

Much greater progress has been made in the study of Mendelism in plants and animals than in man, as it is of course not possible to conduct experiments with human beings in the same way as with plants and animals. Moreover, we know that most human beings are very complex hybrids, and this in itself makes it difficult to study inheritance in man. Also, man is a slow-breeding animal, so that it has been impossible for modern students of heredity to observe many generations, while it is difficult to get accurate descriptions of characteristics of generations that have died.

Many human characters which seem to behave in Mendelian fashion have been catalogued. Among these are curly hair dominant over straight hair, dark hair over light hair, brown eyes over blue eyes, normal pigmentation over albinism, and normal condition over hereditary insanity or feeble-mindedness. In crosses between the negro and the white, color of skin does not act as a simple character dependent on one factor. In the F_2 and subsequent generations, however, there may be individuals much lighter or much darker in color than the mulatto parents. Indeed, the color may be as dark as that of a negro or light enough to pass for white.

These results indicate that the color is conditioned by multiple factors which act in Mendelian fashion. In a previous connection we have seen that if three cumulative factors are concerned, then in the F_2 generation each of the original races would be represented by only one individual out of sixty-four, while sixty-two would be intermediate; if six factors were concerned, only one out of 4096 individuals of the F_2 generation would have the germinal composition of each original race.

PLANT BREEDING

Selection. The method of obtaining improved varieties has been that of selecting plants with desired characters for propagation, and discarding undesirable ones. Of course, the act of selecting individuals with desirable characters cannot produce anything new, as selection presupposes variations which can be selected. In order to learn how new varieties are produced it is necessary, therefore, to consider the origin of variation. *Variation* is a universal phenomenon among both plants and animals — so universal, in fact, that it has given rise to the common expression that no two plants or animals are alike.

Acquired characters. Favorable methods of cultivation frequently result in the production of larger and more vigorous individuals. If a plant attains to an exceptionally large size by growing under unusually favorable conditions, this size is said to be an acquired character, as it is one acquired during the life of the individual and not one that the individual inherited. Such acquired characters do not appear to be inherited. The seeds of vigorous plants are likely to be larger than those of weak plants; large seeds contain more stored food than smaller ones, and so give the seedlings a better start. In this way the offspring of a vigorous plant may be somewhat larger than the offspring of a less vigorous one. This character, however, is not hereditary, as the larger size will be maintained only so long as each generation is grown under the favorable conditions that gave rise to this exceptional vigor.

Continuous variations. The variations between plants are of different kinds. Some are minor variations, known as continuous variations, which are not inherited. When many plants of one homozygous variety are examined, it is found that they differ from one another by slight variations which are quantitative in character and do not depart from the average beyond a certain limit. Thus, some plants will be shorter and others taller, some will have deeper-colored and others lighter-colored flowers, etc. While the plants of one generation may vary thus among themselves, the average for large numbers will be constant for different generations. Continuous variations are largely or entirely due to environmental conditions. They are said to be continuous because between any two variations there is a gradual series of variations which differ from one another by imperceptible gradations. Continuous variations are also called fluctuating variations, because in successive generations the character fluctuates around the same average.

The selection of fluctuating variations cannot produce varieties with different hereditary characteristics, because when an extreme type is selected the progeny always tend to return to the average. The most that can be accomplished by selecting such variations is to produce a quantitative change while the selection is continued. If during several succeeding generations the seeds of the tallest plants of a variety are selected for propagation, we may get taller plants than the average, but this extra height will disappear as soon as selection is discontinued.

Hybrids. Hybrids are the offspring produced by the union of the sexual cells of different genera, species, or varieties. The offspring resulting from the crossing of white-flowered and red-flowered plants of the same species are examples of hybrids, as are also the offspring obtained by crossing different genera, as the radish and the cabbage. In general, crosses are most easily made between closely related races. When the races are not closely related the hybrids usually show a lessened fertility or absolute sterility, while hybrids formed by crossing distantly related species are frequently lacking in vigor.

Variations due to hybridization. When two varieties of plants which differ from each other in a number of characters are crossed, their offspring will usually show some of the characters of each parent, while those characters which are recessive and do not appear in the F_1 generation will do so in subsequent generations. Hybridizing, therefore, tends to produce variations. A knowledge of the Mendelian laws of inheritance enables us to combine hybridizing and selecting much more intelligently than we could otherwise do. We have seen that a cross between tall peas with round yellow seeds and dwarf peas with wrinkled green seeds gives, in the F_1 generation, tall plants with round yellow seeds, as the characters tall, round, and yellow are dominant over the alternative characters. If it were desirable to have dwarf plants with round yellow seeds, these could be obtained in the F_2 generation. In this generation one out of sixty-four individuals would be homozygous for dwarf, round, and yellow. The progeny of these individuals would therefore breed true. The F_2 generation would also contain dwarf individuals with round yellow seeds which would not breed true. Such plants would be heterozygous for round or yellow or for both of these characters. In order to distinguish between the plants which are homozygous for the desired characters and those which are heterozygous it is only necessary to obtain a sufficient number of plants of the next generation and see which plants breed true. This example enables us to see how we can combine the desirable characters of one variety with those of another and get a variety that is superior to both of the parent varieties.

Mendelism also shows that certain characters are the result of a heterozygous condition, and that we cannot obtain a variety that will breed true for such characters. Pink four-o'clocks afford a good example. As pink flowers are produced only by heterozygous individuals, pink-flowered plants will never breed true but will produce red-flowered, pink-flowered, and white-flowered plants in the ratio of one, two, and one.

Mutations. It has been pointed out that the selection of continuous variations does not result in hereditary changes, while hybridization may produce new varieties. There are, however, variations which are not the result of hybridization and which are hereditary. These may occur even in pure lines, that is, in strains descended from a single self-fertilized homozygous individual. Such hereditary variations are much less numerous than are fluctuating variations, and are known as mutations. Characters which appear as the result of mutations are inherited in Mendelian fashion and may be either dominant or recessive. In popular language, mutations are frequently spoken of as sports.

The improvement of cultivated plants has frequently been due to the selection of mutations. Red sunflowers and giant varieties of tobacco are examples of mutations.

A character which results from a mutation may be considered as due to the modification of something already present rather than as the result of the addition of an entirely new factor. A mutant may vary greatly or only slightly from the parent.

The red sunflower affords a good example of a mutant. In the sunflower the so-called flower is in reality a head composed of many flowers packed close together. The central, or disk, flowers are small, while the outer, or ray, flowers are large and have a brilliant orange color. It is these ray flowers that are largely responsible for the attractive appearance of the head. In the year 1910 a sunflower with chestnut-red rays was found by a roadside in Boulder, Colorado. The plant was very striking, and its presence could only be explained as due to mutation. In order to reproduce the plant it was necessary to cross it with a plant having ordinary orange-colored rays, as sunflower plants are not fertile unless cross-pollinated. In the F_1 generation of this cross about half the plants were red and the other half orange. Subsequently the red color proved to be a Mendelian dominant. Therefore the explanation of the fact that in the F_1 generation of the original cross half the offspring showed the red color and half the orange color would seem to be that the original red mutant was heterozygous and contained only one factor for red.

An examination of the red color of the red sunflowers showed that the chestnut-red color was due to the fact that both a red pigment and the original orange pigment were present in the rays. By subsequent breeding, plants were obtained that had rays with the red and without the orange color. These flowers were wine red or old rose. The breeding was carried out in the following manner:

Since the year 1889 there has been in cultivation a variety of sunflower called primrose, which arose as a mutant from the ordinary orange variety, and which is pale yellow. This variety was crossed with the chestnut red. In the F_1 generation the offspring were all chestnut red, as the orange color dominates the pale yellow and the red dominates the absence of red. In the F_2 generation there were four kinds of plants obtained: chestnut red, orange, wine red, and light yellow, approximately in the proportion of nine, three, three, one. This is the dihybrid ratio and shows that in this case we are considering two pairs of independent unit characters. The first pair is the dominant red, R, and the recessive, which is the absence of

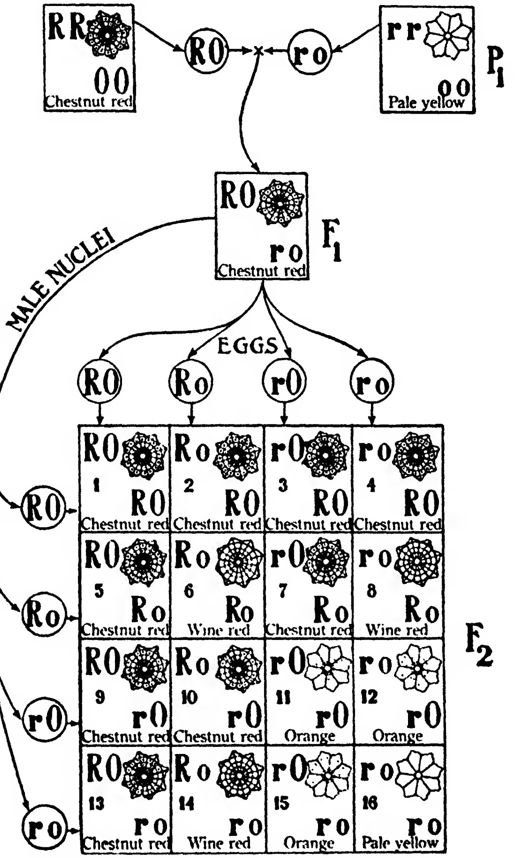


Fig. 404. Diagram of inheritance of flower color in sunflower

R represents a factor for the dominant character red; r, the absence of this factor; O, the factor for the dominant color orange; and o, the factor for the recessive pale yellow. R and O together produce chestnut red

red, r; the second pair is the dominant orange, O, and the recessive pale yellow, o. By these symbols Fig. 404 shows the crossing of the chestnut red and the light yellow and the composition of the F_1 and F_2 generations. The red sunflower shows how a new variety can arise as a mutation, and how still other new varieties can be obtained by further breeding.

Character of mutation. Mutations may result in striking new characteristics, as in the case of the red sunflower. The difference may be one of color, form, size, or other features. A quantitative change may be conspicuous. The evening primrose has by mutation produced large forms. Often, however, a mutant form may differ only very slightly from its parents. The mutation may result in only a very slight difference in size, or a change in shade of color, or some other minor difference. The essential characteristic of a mutation is that there is a change which is hereditary.

Origin of mutations. Mutations are due to alterations in chromosomes. In a large number of cases a mutation is connected with differences which have been observed between chromosomes of the mutant and those of the parent. Many mutants are connected with changes in the number of chromosomes. The large *gigas* forms of the evening primrose have twice the number of chromosomes found in ordinary plants. In other words, instead of being diploid the plants are tetraploid. Many cultivated plants have varieties with more than the diploid number of chromosomes. These multiplications of the original number may be triploid, tetraploid, pentaploid, hexaploid, etc. Plants with more than the usual number of chromosomes are sometimes larger than the parent form, but this is not always the case. They may also differ in other characteristics. The most common cause of the origin of tetraploid varieties, probably, is that the chromosomes of a nucleus have divided but the nucleus itself has not. Various other irregularities in chromosome numbers have been found to be connected with mutations. Thus, mutations may have $2x + 1$ or $2x + 2$ chromosomes; such numbers appear to be derived, at least in some cases, from the failure of a chromosome to divide at the usual time. If two chromatids do not separate at metaphase but pass together to one pole and thus enter a single nucleus, that nucleus will have one more than the usual number of chromosomes, while its sister nucleus will have one less. Modifications of individual chromosomes have also been noted in mutants. While changes in chromosomes can thus be observed in many mutants, it is very frequently the case that there is no observable change. It would appear, however, that in such cases there must have been an alteration in a chromosome, even though this change may have been purely chemical and one which cannot be detected by any means at our disposal. We know that the inheritance of Mendelian characters is dependent on chromosomes, and we have definite evidence that many mutations are due to changes in chromosomes; therefore it seems logical to conclude that, in general, mutations are brought about in this manner.

While it does appear that changes in chromosomes are responsible for mutations, we are still left with the problem of the cause of the changes in the chromosomes themselves, and this is one of the most perplexing problems of heredity and evolution. A mutation often occurs in a single individual raised with many others under as uniform conditions as the experimenter can produce. Mutations have been induced by subjecting organisms to such violent treatments as exposure to X rays, radium, or excessive temperatures. These experiments do not solve the problem of the cause of mutations under natural conditions, as the doses of X ray and radium employed are much greater than the organisms would ever encounter under natural conditions. They do show, however, that in some cases mutations are caused by definite stimuli.

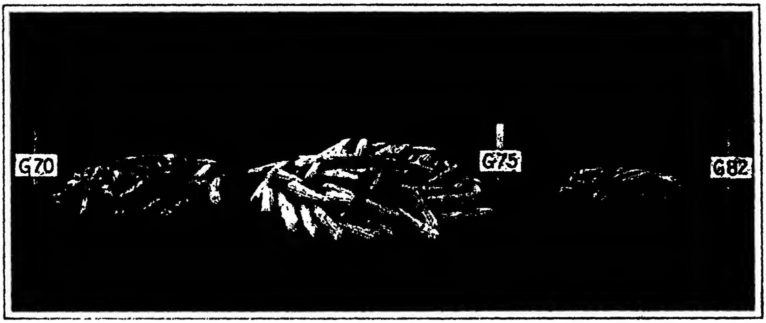


Fig. 405. Hybrid vigor in corn

Right and left, two inbred strains; center, their F_1 progeny. (After Shull)

Hybrid vigor. The crossing of two races which are not too distantly related frequently results in an increased vigor, known as hybrid vigor, in the offspring (Fig. 405). In wide crosses there is often an increased vigor accompanied by sterility, as in the well-known case of the mule; in very wide crosses sterility may be accompanied by a lessened vigor; while if the germinal composition of two races is too dissimilar, it is impossible to hybridize them.

Within the range in which crossing results in an increased vigor without lessened fertility, the vigor increases with the degree of heterozygousness resulting from the cross. Self-fertilization of a heterozygous race results in a decrease in the heterozygous condition; so, as might be expected, self-fertilization of a vigorous hybrid race results in a decrease in vigor which continues until a homozygous condition is reached, after which there is no further deterioration.

Hybrid vigor appears to be connected with the fact that the hybrid contains the dominant factors of both parents, and that in most cases dominant characters are desirable and promote vigor.

Likewise, the deterioration which follows the self-fertilization of vigorous hybrids seems to be connected with a decrease in the number of dominant factors in the homozygous races. Moreover, when a large number of contrasting factors are involved, the linkage of factors in the same chromosome prevents the accumulation in a homozygous condition of all the dominant factors present in the hybrid. Thus, if a chromosome from one parent of the hybrid contained the dominant factors A and B and the recessive factors c and d, and the corresponding chromosome from the other parent carried the recessive factors a and b and the dominant factors C and D, the hybrid would possess all four dominant factors; but it is not to be expected that self-fertilization would result in an individual homozygous for the four factors, A, B, C, and D.

Inbreeding and outbreeding. Self-fertilization, or the crossing of closely related individuals such as brothers and sisters or parent and offspring, is known as inbreeding, while the crossing of unrelated individuals is known as outbreeding.

Inbreeding. The majority of flowering plants are provided with some device for promoting cross-pollination. On the other hand, some vigorous plants, such as wheat, rice, barley, oats, tobacco, beans, and tomatoes, are characterized by very nearly continuous self-fertilization. Self-fertilization in these cases certainly does not appear to be harmful. Therefore we may conclude not only that cross-fertilization is not always necessary, but also that self-fertilization is not necessarily harmful.

It would seem that continuous vegetative propagation without any sexual reproduction is also without deleterious effects. Ordinary varieties of bananas, pineapples, and horseradish are examples of very vigorous plants that are always reproduced vegetatively. Moreover, they have reproduced in this manner throughout the whole period during which we have knowledge of them. As far as hereditary composition is concerned, vegetative reproduction and self-fertilization of homozygous strains should have the same effect.

Self-fertilization in corn. Vigorous varieties of corn have been found to be complex hybrids. Self-fertilization of such varieties results in rapid deterioration. This deterioration is most marked in the F_1 generation. The deterioration continues for several succeeding generations, but the amount of deterioration becomes less and less. The final result is the production of approximately homozygous strains which differ greatly from each other. When, as a result of self-fertilization, the strains become homozygous, no further deleterious effects are produced by self-fertilization. When the deteriorated homozygous strains are crossed, the vigor of the original plants is restored (Fig. 405). This result shows that the deleterious effects following self-fertilization were the result of reducing the plants to a homozygous condition. Crossing the deteriorated strains restored the heterozygous condition, in which the unfavorable recessive characters were again masked by favorable ones.

Deleterious effects of inbreeding. If a strain contained no unfavorable recessive characters, self-fertilization could not cause the appearance of any such characters. The valuable strains in such self-fertilized plants as wheat and beans appear to be homozygous, and self-fertilization cannot produce deterioration by permitting the appearance of unfavorable recessive characters. We may conclude, therefore, that self-fertilization can produce no harmful effect in homozygous strains, but that it can do so in strains which are heterozygous, as it decreases the number of dominant factors and also allows unfavorable characters to appear. It is apparently for this reason that harmful results frequently follow the close mating of domestic animals and of man. These are usually complex hybrids and frequently carry unfavorable recessive factors which are masked by favorable dominant ones.

The crossing of two separate individuals, which is characteristic of cross-pollinated plants and of all higher animals, has a tendency to promote a heterozygous condition, and an increase in heterozygousness is frequently associated with increased vigor. Self-fertilization, or close inbreeding, has a tendency to produce a homozygous condition, and so frequently results in decreased vigor in species that are normally cross-fertilized and heterozygous.

The value of outbreeding. Outbreeding frequently affords a great advantage over inbreeding in that it results in increased vigor, and also because it permits the combination of characters of different varieties. The vigor of the F_1 generation of a cross is frequently utilized in breeding. A conspicuous example is that of the mule, obtained by crossing a mare and a male ass. In plants many valuable hybrids are reproduced vegetatively by buds or by cuttings. This method of preserving a hybrid is very frequently practiced with fruit trees and ornamental plants.

While crossing different strains frequently results in increased vigor, it does not follow that a good variety will be improved by crossing with a poor one; in fact, the reverse is usually the case. It is not to be expected, of course, that a valuable variety can be improved by the incorporation of undesirable characters in it.

Combination of outbreeding and inbreeding. When a plant can be reproduced readily by vegetative means, it is a simple matter to retain the desirable characters found in a hybrid. The case is very different, however, with organisms that are reproduced only by the sexual process. In such cases, if a hybrid is heterozygous for many desirable characters, a strain that will breed true for a considerable proportion of them can frequently be obtained by inbreeding. Very valuable results may be produced by such inbreeding accompanied by vigorous selection.

CHAPTER XVI

DIVISIONS OF THE PLANT KINGDOM

Classification of plants. In any consideration or study of plants it is necessary to classify them, that is, to arrange them in groups and subgroups. The different species are placed in the various groups and subgroups according to their similarities and differences. That part of botany which deals with the classification of plants is known as *systematic botany.*

Since the general acceptance by botanists of the theory of evolution, it has been the ideal of systematic botanists to devise a classification which will show the true relationship of the different kinds of plants. Great progress has been made in this direction; but on many points there is a dearth of information, and considerable speculation and divergence of opinion. There is also some disagreement owing to the tendency of some authorities to prefer large groups with many members and of others to have many small groups with fewer components.

Divisions of the plant kingdom. A very widely used system of classification of plants is one which divides the plant kingdom into four large groups called divisions or *phyla.* These are *Thallophyta, Bryophyta, Pteridophyta,* and *Spermatophyta.* These names end with the suffix *phyta,* which denotes that they are names of divisions of the plant kingdom.

Spermatophyta. The division *Spermatophyta* includes all seed-bearing plants. Some plants, such as seedless bananas and seedless oranges, are regarded as spermatophytes although they do not produce seed. This illustrates the fact that the classification is based on relationship rather than on arbitrary characters. Such seedless plants are so similar in general characteristics to other spermatophytes as to leave no doubt of a close relationship, and in some cases seedless varieties have arisen from seeded ones under circumstances which are well known.

Pteridophyta. The pteridophytes are the ferns and their allies the horsetails and clubmosses (Figs. 859, 882). They have neither flowers nor seed, but reproduce by means of single cells known as *spores*. On the backs of the mature leaves of most of the common ferns are raised brown patches. In these are many spore cases (*sporangia*), each containing numerous spores. The spores fall to the ground and give rise to minute plants called *prothalli*, singular *prothallus* (Fig. 831). The prothalli produce eggs and motile male cells, the *spermatozoids* (Fig. 832). An egg is fertilized by a spermatozoid and then develops into the familiar fern plant (Fig. 837). There is thus an alternation of a large plant which produces asexual spores and a minute plant bearing sexual cells. This alternation is known as the *alternation of generations*, the alternate generations being asexual (spore-bearing) and sexual.

Bryophyta. The bryophytes are the mosses and the mosslike plants called liverworts.

Thallophyta. The name *Thallophyta* indicates plants with thallus bodies, that is, not differentiated into stems, roots, and leaves. A great variety of such plants are found in the division *Thallophyta*. These include the bacteria, blue-green algae, algae, fungi, and lichens.

The system of classification which divides the plant kingdom into four divisions was devised many years ago when botanists knew much less about the variety in smaller plants than they do today. Further study has shown that the old division *Thallophyta* should be divided into a number of divisions or subdivisions, as it embraces a great diversity of plant forms, some of which, as for instance the bacteria and the true algae, can be separated by much more fundamental features than the bryophytes, the pteridophytes, and the spermatophytes. But even botanists who make several divisions of the *Thallophyta* often say "*Thallophyta*" and "thallophytes," as these are very convenient terms and are easily understood, being based on obvious characteristics.

In this book the thallophytes are divided into various divisions according to modern ideas of classification and are given names ending with the suffix "phyta." It is perhaps more scientific to consider these as independent divisions, but they can be regarded as subdivisions of the *Thallophyta*.

Classes. Divisions are subdivided into *classes.* Thus, the division *Spermatophyta* is composed of the classes *Gymnospermae* and *Angiospermae,* which are separated by prominent characteristics. The angiosperms are the flowering plants and have their seeds enclosed in ovaries. The gymnosperms include the cycads and conifers; they lack true flowers, and their ovules and seed are not enclosed in ovaries, but are said to be naked. In many gymnosperms, as in the pine, the seeds are borne in cones. At the time of pollination the scales of the pine cone are separated so that the pollen may reach the ovules. After pollination the scales close together, to open again when the seeds are mature. However, this is very different from the enclosure of the ovules and seed in an ovary as in angiosperms.

Orders and families. Classes are in turn divided into *orders,* the names of which end in *ales.* Thus, the roses belong to the order *Rosales.* Orders are further divided into *families,* the names of which usually end in *aceae,* as *Rosaceae,* the rose family.

In a few cases the family name does not end in *aceae,* the name of the palm family being *Palmae.*

Families are composed of *genera,* and these, in turn, of *species,* the latter being the individual kinds of plants. Species are designated by the use of both the generic and specific names, the generic being given first and the specific after it. This has been discussed in Chapter I.

Influence of fossil botany. The classification of plants was originally based on living forms. However, a study of the plants of past geological ages has given a great deal of information on the subject. Large groups which were formerly dominant have diminished in importance until they are represented by a few small forms; other large groups, which throw much light on the relationship of living plants, have disappeared completely. Therefore some knowledge of fossil plants is necessary for an understanding of the classification of plants. For this reason we will discuss briefly the nature of fossils and the sequence of geological ages before considering the different divisions and classes of plants.

Nature of fossils. A fossil may be defined as any impression, remains, or trace of a plant or animal of a past geological age. The most important types are impressions and petrified structures.

We are all familiar with the impressions made by leaves in mud. Plants and animals are frequently buried and leave impressions. If these impressions remain after the material in which they are made is turned to rock, the result is a fossil. Again, plants may be enclosed by incrustations of silica or lime from the water of hot springs. The impressions (Figs. 406, 407) give us much information concerning the form and shape of organisms or organs, but usually nothing of their internal structure.

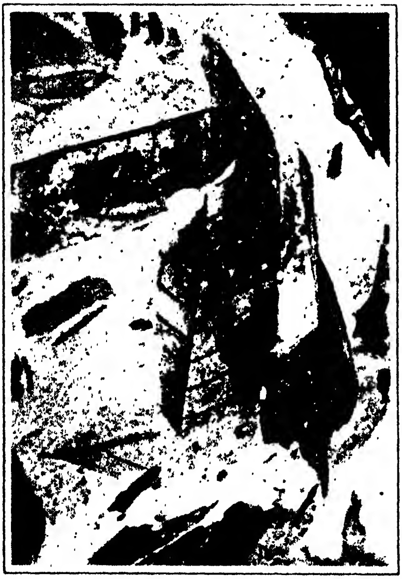


Fig. 406. Fossil leaves

Among the most instructive fossils are those produced by petrifaction. In such cases the plant or animal material has decayed slowly in water in which a large amount of silica, lime, or other mineral matter was dissolved, and the organic matter has been replaced by the mineral in solution. It has often been found possible to study the microscopic structure of these fossils in great detail.

In addition to the above classes of fossils we sometimes find the original material of organisms preserved. Rarely a complete structure, such as a leaf, may be removed from the enclosing rock. Even when the material is in a carbonized condition it may afford valuable information.

Formation of fossils. The rocks of the earth's surface are divided into two classes, according to their origin: igneous and sedimentary. Igneous rocks are produced as the result of heat, and do not contain fossils. Sedimentary rocks are formed by the transportation of small rock particles and their subsequent deposition in another place, or they are the result of precipitation from solution, or of secretion by organisms, as in the case of limestones. Sedimentary rocks are the ones that yield fossils.

It is a common observation that most dead plants and animals are quickly destroyed by decay. They are not likely to be fossilized unless they are rather quickly covered by some protecting material. Also, oxygen must be largely excluded, as decay is dependent on oxidation. Such favorable conditions are most usual in lakes, seas, or marshes. Organisms with hard parts are much more likely to be fossilized than are those without them; for this reason the very primitive and soft plants and animals are rarely fossilized.

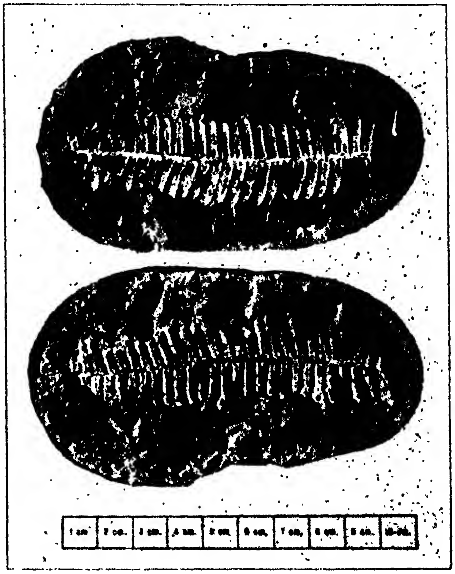


Fig. 407. Fossil leaf

Age of fossils. In the formation of sedimentary rocks the oldest naturally occur at the bottom of the series and the youngest at the top. The most ancient fossils will be found in the oldest rocks, while the most recent fossils will be in the youngest rocks. In the past history of the earth, areas that were under the sea have risen and become dry land (Fig. 408), while some of the areas that were formerly dry land are now under the sea. Owing to erosion and the washing of materials from the land into the sea (Fig. 409) there is a general tendency for the surface of the dry land to be washed away, while that under the sea is built up by the accumulation of deposited material. In this way rocks are built up while the land is submerged, and are worn away when the land is exposed.

Sometimes the same land has been elevated above the sea more than once. While the land is submerged, layers of rock are formed. When the land is exposed as the result of elevation, the rock begins to be eroded, and if the area is exposed for a long period it may be removed to a considerable depth. If such an area is again submerged, its surface will be covered by new layers of rock. There will be a great difference in age between the lowest of these new layers and the old layer on which it is deposited. This is due to the fact that during the time when the area was exposed no new layers were formed, and much of the former rock, ordinarily of its newest part, was removed. Owing to such occurrences as that just outlined, large gaps frequently occur in the geological records in a given series of rocks. By piecing together the geological records from various parts of the earth, however, it is possible to get much information concerning the relative ages of different rock strata.

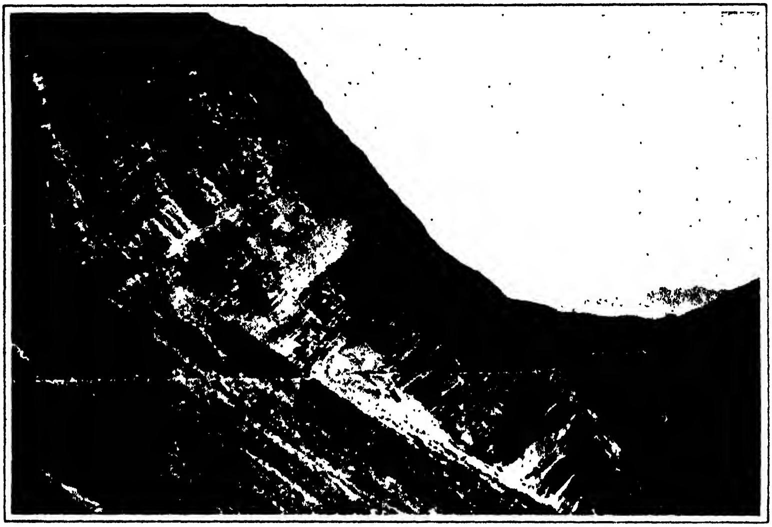


FIG. 408. Cliff more than a thousand feet high composed of alternately bedded sandstone and shales (Mountain Province, Philippine Islands)

Photograph by Dr. H. Otley Beyer

Incompleteness of fossil records. While fossils have been formed in various ways, the great majority of them originated under water, and the discovery of most of them has been due to the emergence of land that was formerly submerged. When such fossils are discovered it is usually owing to a combination of favorable circumstances. Fossils that are formed in deep seas are rarely seen, as such areas are not often elevated sufficiently to become dry land. When areas of fossil-bearing rocks are exposed to erosion, the fossils are uncovered, and in this way many fossils are brought to the attention of man; but those that were exposed in this manner in past ages have been destroyed, and so a great deal of the fossil record has been lost. Fossils have also been destroyed by being dissolved from rocks, by being subjected to great pressure, and by various other means. As was previously stated, the soft parts of organisms are rarely fossilized. Owing to the above-mentioned facts and for other reasons, the fossil record is not as complete as we should like to have it; moreover, the study of such fossils as can be found is very far from complete; yet, in spite of its imperfections, the fossil record has given us considerable knowledge of the past history of floras and faunas.

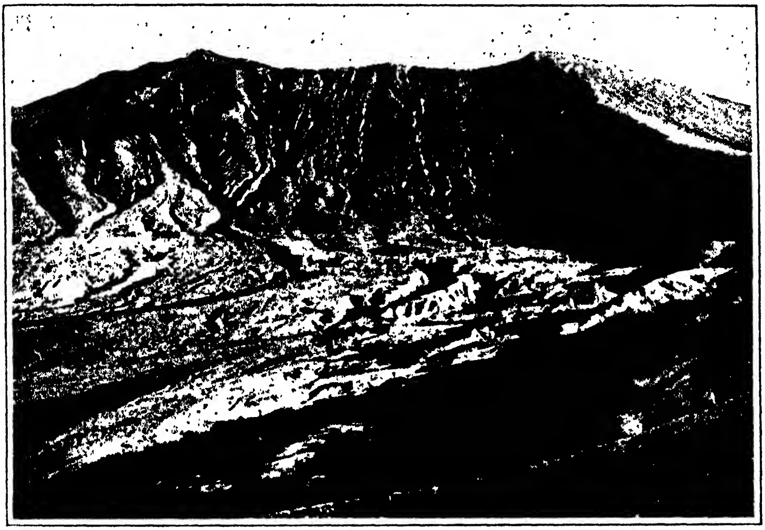


FIG. 409. Erosion on a mountainside (Taal Volcano, Philippine Islands)

Eras and periods. Geological time is divided into five eras: the Archeozoic, Proterozoic, Paleozoic, Mesozoic, and Cenozoic. These eras are subdivided into periods.

According to the best estimates geological time has lasted at least 2,000,000,000 years. About 500,000,000 years have elapsed since the dawn of the Paleozoic era.

In Fig. 410 the different eras and the periods of the more recent eras are shown in tabulated form, also the dominant plants and animals of the different ages. Several of these periods are subdivided into two periods by many geologists.

The most accurate method of estimating the age of the earth is based on the fact that the radioactive elements uranium and thorium disintegrate spontaneously, forming lead, at constant rates which can be determined. The age of a uranium mineral can therefore be calculated from the proportions of uranium and lead it contains. In actual practice there are various complications which must be taken into account; in fact, conditions for accurate determinations of age are so exacting that only a few have been made. As estimated by this method, one ore has an age of more than 1,800,000,000 years. This ore is in dikes that are intruded into older rocks, and so it may be concluded that the age of the earth is at least 2,000,000,000 years. The age of a mineral accurately dated as belonging to the latest Cambrian has been determined as 450,000,000 years, and from this evidence it has been estimated that the Paleozoic era began about 500,000,000 years ago.

A great deal about the relative and something of the actual lengths of ages and periods can be calculated from the thickness of sedimentary rocks formed during them. Recent figures obtained in this way agree with those calculated from radioactive disintegration, and so we can estimate the duration of various ages. However, so much information is lacking that it may be a long time before these estimates are very exact.

History as told by fossils. The fossil record shows that in animals there has been a development from the simple to the complex, and that mammals appeared late in geological history. In popular language certain successive geological times are often called the Age of Invertebrates, the Age of Fishes, the Age of Amphibians, the Age of Reptiles, and the Age of Mammals. The great groups of animals appeared in the above order and were dominant in the ages which bear their names. Most animals of the earlier ages, such as gigantic amphibians and reptiles and the birdlike reptiles, have disappeared; many of them have left no descendants or close relatives.

Incomplete as a fossil record is, it leaves no doubt that the plants and animals of one age were derived from those of a previous age by gradual changes, and that the accumulation of these changes through the long periods of geological time has resulted in an evolution from very simple ancestors to complex organisms.

Dominant Plants	Era	Period	Dominant Animals	Estimated Age in Years
Flowering plants	Cenozoic	Recent Pleistocene } Quaternary	Man	60 million
		Pliocene Miocene Oligocene Eocene } Tertiary	Mammals	
Gymnosperms	Mesozoic	Cretaceous Jurassic Triassic	Reptiles	120 million
Giant spore plants and seed ferns	Paleozoic	Permian Carboniferous	Amphibians	320 million
Ancient spore plants		Devonian	Fishes	
Algæ		Silurian Ordovician Cambrian	Invertebrates { Sea scorpions Mollusks Trilobites	
Blue-green algæ	Proterozoic		Evolution of invertebrates	Not less than 1500 million
Very simple plants including bacteria	Archeozoic		Evolution of unicellular animals	

Fig. 410. Geological ages and periods

The earliest known plants had very simple structures; age by age, more and more complex forms made their appearance (Fig. 410). The only plants of which there is anything like good evidence before the Paleozoic age are the bacteria and blue-green algae, and these are the two simplest classes of plants. True algae are the highest types found in the earlier Paleozoic rocks. The most ancient known representatives of the land plants are very primitive pteridophytes from the Devonian period. During the succeeding Carboniferous period there was a great diversity of pteridophytes, some of which were large, complex, and dominant trees. The first known seed plants are from late Devonian times. They belonged to the most primitive class of gymnosperms, the seed-ferns. This group became extinct in the Mesozoic age. Angiosperms are not known earlier than the Cretaceous, the last period of the Mesozoic age. During this period they rose to dominance, and they have retained this position since that time.

CHAPTER XVII

BACTERIA

STRUCTURE

General characteristics. The bacteria are exceedingly minute and very simple organisms. Most of them are essentially single unbranched cells (Figs. 411, 412), although many adhere together in small groups or chains (Figs. 411), a few have branched cells (Fig. 417), while some are characterized by occurring as filaments (rows of cells). Even when bacteria are held together in groups or chains, each individual cell carries on its own life processes independently of the others; there is no division of labor. The unbranched single-celled bacteria have the general shape of balls (*coccus* forms), rods (*bacillus* forms), or curved cells (*spirillum* forms) (Fig. 411).

Size. The size of microscopic objects is usually measured in terms of microns, which are denoted by the Greek letter μ; the name of the letter is "mu." A μ is a unit of length, .001 of a millimeter. Most bacillus forms are between 1.5 and 10 μ in length. Perhaps an average size would be about 2 μ in length and .5 μ in diameter. Coccus forms are usually about .5 or .6 μ in diameter.

If we assume a rod-shaped bacillus to have the shape of a cylinder, its volume can be calculated by the formula $\pi r^2 \times$ length. The calculated volume of a bacillus $.5 \times 2\ \mu$ is .000,000,000,393 cu. mm. Assuming the specific gravity of the bacillus to be 1.04, it would weigh .000,000,000,408 mg.

Number of bacteria. Although we do not see the bacteria, they are present all around us. They float in the air to great elevations, occur on the surfaces of almost all objects, and are very abundant in water and soil. They are numerous on our skin and occur in enormous numbers in our mouths and intestinal tracts. The number of bacteria in various natural situations is very great. They may occur by the thousands in a cubic centimeter of water or milk.

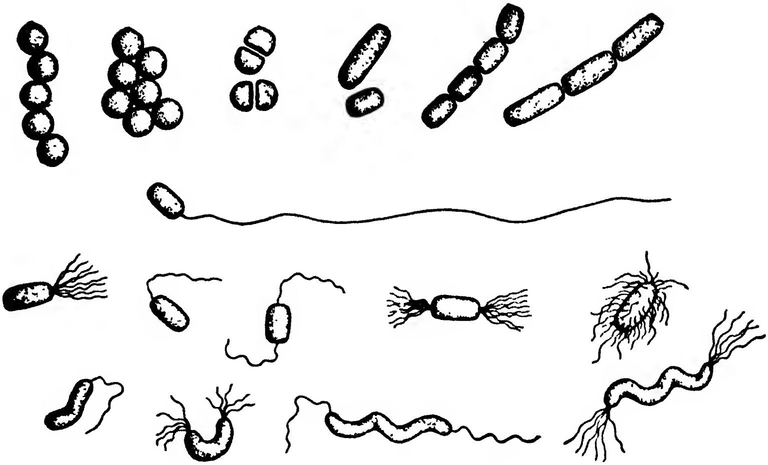


Fig. 411. Various forms of bacteria

First line, at the left, coccus forms; at the right, bacillus forms; second and third lines, bacillus forms; fourth line, spirillum forms

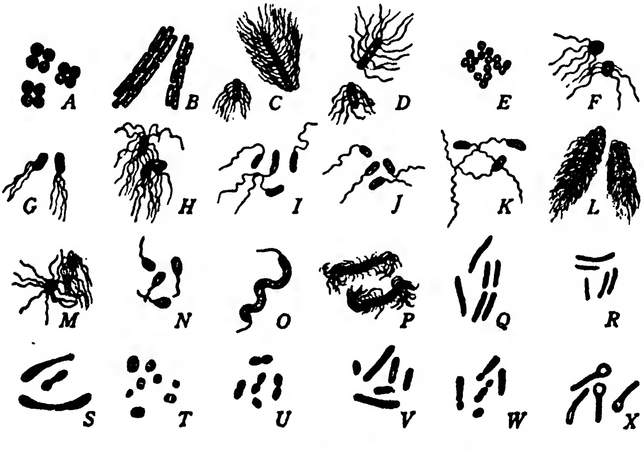


Fig. 412. Various types of bacteria

Among those which cause serious diseases are *B*, anthrax; *E*, boils; *H*, typhoid fever; *N*, cholera; *Q*, tuberculosis; *R*, leprosy; *S*, diphtheria; *T*, meningitis; *U*, pneumonia; *V*, dysentery; *X*, tetanus

Normal soils with a good percentage of organic matter contain, on the average, from two million to two hundred million bacteria per gram. Heavily manured soils may contain more, poor soils less. Manure and sewerage may contain a great many more.

Cell structure. The bacteria are small masses of protoplasm without chlorophyll, surrounded by cell walls. The bacteria do not possess nuclei such as are found in higher plants, but many of them contain granules which have staining properties resembling those of chromatin (Fig. 413). In many cases these granules are scattered throughout the cell, while single spherical, spiral, or zigzag structures have been described in some bacteria. The question as to whether or not the bacteria have nuclei seems to depend largely on the definition given for a nucleus. If the term nucleus is confined to those highly organized nuclei which divide mitotically, then the bacteria do not appear to have nuclei. If, on the other hand, granules which have staining properties resembling those of chromatin may be regarded as nuclei, some bacteria possess such structures. Certainly the bacteria do not seem to possess anything that resembles a typical nucleus.

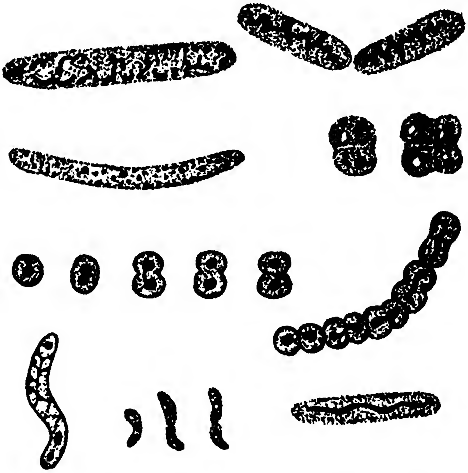


FIG. 413. Internal structure of bacteria

Redrawn after Dobell

A few of the cocci and many of the bacilli and spirilla have very small, delicate, threadlike processes known as flagella (Figs. 411, 412). The movements of these flagella give the bacteria the power of locomotion.

The small size of the bacteria makes their structure difficult to observe, and the flagella are so minute and delicate that there is still considerable debate as to the presence or absence of flagella in many common bacteria. Naturally it is difficult to study their nature. They are thought to be extensions of the protoplasm through the cell wall.

The cell wall is a delicate membrane which cannot be seen in bacteria in their natural state. It may be made visible by plasmolyzing the cell so as to separate the cell wall from the protoplasm. It is difficult to demonstrate the presence of the cell wall by staining, as it and the protoplasm are colored by the same aniline dyes. This similarity in staining reaction indicates a similarity in composition which is not found in higher plants. The chemical nature of the wall is a debated question. In some bacteria it is reported as showing a blue color when treated with chloride of zinc. This reaction is often used as a test for the presence of cellulose or hemicellulose. The presence of cellulose has been reported by several observers, while others have failed to find it. In some bacteria the principal chemical elements found in the wall occur in about the same proportions as in chitin, thus suggesting a relation to chitin. Apparently the composition is not the same in all bacteria, and the whole question needs further investigation.

Capsules. In addition to a thin layer of cell wall surrounding the protoplasm, there is in some bacteria an external covering or capsule of slime which is derived, at least in some cases, from the external layer of the cell wall. In certain forms this is relatively thick in comparison with the size of the cell. In some species the capsule may or may not be present, depending upon the conditions under which the bacteria are growing. The capsules are useful in identifying some bacteria.

Cell inclusions. Some bacteria are distinguished by the presence of characteristic inclusions. Bodies known as metachromatic granules are common in large bacteria. In bacillus types they often occur as large "polar bodies"; in this form they are prominent in the diphtheria bacillus. Their presence and arrangement is often used in the identification of bacteria.

"Acid-fast particles" are characteristic of certain bacteria and afford a convenient method of distinguishing them. Among such bacteria are the tuberculosis and leprosy bacilli. The acid-fast particles are difficult to stain with aniline dyes, and after being stained they resist the decolorizing action of acids, from which fact they get their name. Bacteria which are characterized by the presence of these particles are known as acid-fast bacteria.

Glycogen and fat are found in some bacteria; granules of sulfur are found in sulfur bacteria.

REPRODUCTION

Multiplication. No sexual reproduction is known among bacteria. They multiply by the simple process of division. A constriction appears around the middle of the cell, and the protoplasm is divided into two parts by an ingrowing cell wall. Bacillus and spirillum forms divide across the middle of the cells at right angles to their long axis. After division, the daughter cells grow in length until they reach mature size. If the daughter cells do not separate immediately, chains of varying length may be formed. Coccus forms assume an ellipsoidal figure before dividing; the daughter cells are at first flattened against each other, and then round out as they separate.

Various coccus forms divide in either one, two, or three planes. Those that divide in only one plane (*Streptococcus*) may hang together to form chains; those which divide in two planes (*Planococcus*) produce flat plates; those which divide in three planes and remain together (*Sarcina*) produce cubical bales or packets. Division in three planes irregularly placed with reference to each other (*Staphylococcus*) produces irregular groups. Coccus forms characterized by occurring in pairs are known as *diplococci* (Fig. 411).

Rate of multiplication. The rate of multiplication varies both with the species and with the environment. Under favorable conditions some bacteria may reach maturity and divide in twenty minutes, others in half an hour. If the latter rate were maintained, the descendants of a single bacterium would be 4 in an hour, 256 in four hours, and about 281,475,000,000,000 in twenty-four hours. If such bacteria were .5 μ in diameter and 2 μ in length, they would still weigh less than 115 grams at the end of this first twenty-four hours, but at the end of another twenty-four hours they would have a weight of more than 32 trillion tons. Of course no such multiplication ever takes place in nature, as the food supply would quickly become exhausted and conditions would rapidly become unfavorable in other respects. Such figures as those given above are not worth remembering; but they serve to emphasize the small size of the bacteria and the rapidity with which they may increase. They also explain why it is that processes which are due to bacterial action, such as souring of milk and decay, may go unnoticed for some time and then seem to take place very quickly, the bacteria being comparatively few at first and later becoming exceedingly numerous.

Spores. Some of the bacilli and a few of the spirilla form *spores*. Spores are defined as single-celled reproductive structures. Those of the bacteria are called *endospores* because they are formed within a cell (Fig. 414). The spore is first seen as a minute spot more refractile than the remainder of the protoplasm. This grows and assumes a position characteristic of the species; that is, terminal, central, etc. The spore becomes surrounded by a thick membrane, and the part of the bacterium exterior to it disintegrates and disappears. The endospores are very resistant to adverse conditions such as dryness or extreme temperature. The spores of the anthrax bacillus have been found to be alive and capable of growing after a lapse of seventeen years, and those of tetanus bacillus after eleven years. When placed under favorable conditions, a spore changes back to an ordinary bacterium. Usually the spore enlarges, some part of the wall dissolves, and the contents emerge as a single bacterium. The importance of spores, from the standpoint of the bacteria, seems to lie in the fact that they enable the bacteria to survive under adverse conditions. As a bacterium forms a single

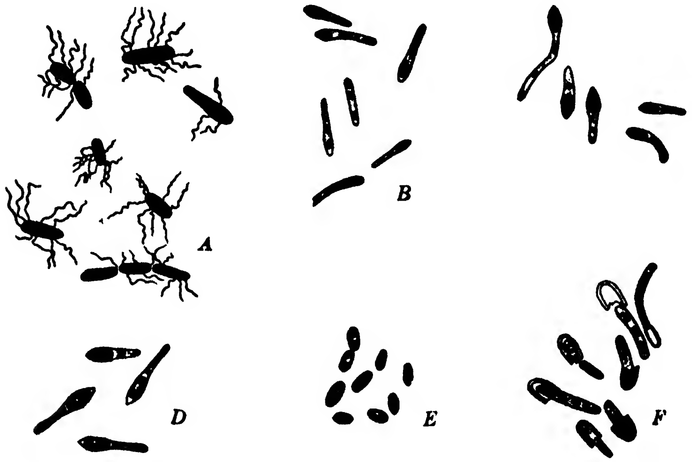


Fig. 414. Spore formation and germination in *Bacillus esterificans*

A, the swarming stage; *B*, *C*, *D*, progressive stages in endospore formation; *E*, spores after the disintegration of the remainder of the bacterium; *F*, the germination of spores. (After Huss) spore and this again gives rise to a single bacterium, spore formation does not result in multiplication, but in survival under adverse conditions.

The success obtained in pasteurization of milk by heating it at 65° C. for twenty minutes is due, to a considerable extent, to the fact that the bacteria responsible for intestinal diseases do not form spores.

A few bacteria which are responsible for human diseases produce spores, as the tetanus organism, which is widespread and responsible for fatal infections in wounds, particularly deep ones; *Clostridium* (*Bacillus*) *welchii*, which is a frequent cause of gangrene in wounds; *Bacillus anthracis*, the causal agent of anthrax, primarily a disease of animals but relatively common in men who handle animals; and *Clostridium* (*Bacillus*) *botulinum*, which does not infect man but produces a toxin which may be present in foods under certain conditions.

Changes in form. The same species of bacteria may show different forms under different conditions. Thus, the nitrogen-fixing bacteria in the roots of legumes may change from rods to oval swarmers and to irregularly shaped and branching vacuolated bodies. The tubercle bacillus is ordinarily a short rod but may be a long, branched filament. Various bacteria have been made to assume such minute forms that they pass through very fine filters that hold back the better-known coccus, bacillus, and spirillum forms. The changes are not from one species to another, but simply variations within the same species.

NUTRITION OF BACTERIA

Nutrition of bacteria. Green plants are very uniform in their methods of nutrition and of obtaining energy. They store energy through photosynthesis and release it by means of respiration. The condition in the bacteria is very different, as among them we find very diversified methods of obtaining energy. According to their methods of life, bacteria may be divided into *autotrophic* and *heterotrophic* species. Autotrophic bacteria are those which can obtain carbon from the carbon dioxide of the air and their energy from the oxidation of inorganic compounds. Heterotrophic bacteria require a supply of organic matter as a source of both carbon and energy. Some of the autotrophic bacteria can live heterotrophically. There are many different types of autotrophic bacteria, and different groups oxidize different substances, among which are sulfur, hydrogen sulfide, ammonia, nitrites, and hydrogen. Other bacteria oxidize iron and manganese compounds, reactions which have usually been regarded as sources of energy, but the significance of which is still in dispute.

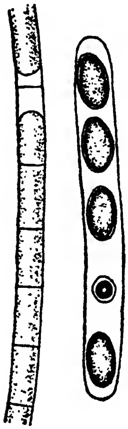


FIG. 415. *Beggiatoa alba*, a sulfur bacterium

Left, filament; right, filament with four endospores and a sulfur globule. (After Ellis)

Autotrophic bacteria. The nutrition of the autotrophic bacteria is strikingly different from that of all other known living organisms. Green plants obtain energy from sunlight and store it in the products of photosynthesis. When energy is required for the life activities of these plants, this stored energy is released by respiration, which is the oxidation of organic compounds that had their origin in the process of photosynthesis. Animals also obtain energy for their life activities by the release, through respiration, of energy stored by plants in the products of photosynthesis. The energy used by both plants and animals is, therefore, the energy of sunlight which is stored by plants in photosynthesis. Both saprophytic and parasitic plants resemble animals in that they obtain energy by the oxidation of organic compounds that had their origin not in themselves but in green plants. The autotrophic bacteria differ from any of the foregoing classes of organisms in that they can obtain energy by the oxidation of inorganic substances existing in nature. It seems very improbable that the first living organisms possessed chlorophyll and obtained their source of energy through such an elaborate process as photosynthesis. The autotrophic bacteria suggest a way in which organisms might have obtained energy before the evolution of either chlorophyll or photosynthesis.

Sulfur bacteria. A number of different morphological and physiological types are found among the sulfur bacteria. However, they are all alike in that they obtain energy from the oxidation of sulfur or its compounds, hydrogen sulfide or thiosulfates. Some of them are filamentous forms (Fig. 415), others are separate cells. Some get their energy primarily from the oxidation of elementary sulfur, others from hydrogen sulfide.

One group of filamentous forms, including the genera *Beggiatoa* (Fig. 415) and *Thiothrix*, oxidizes hydrogen sulfide and accumulates granules of sulfur within the cells. These granules take the place of starch in higher plants as a stored source of energy. If deprived of hydrogen sulfide, the bacteria oxidize the stored sulfur; after this is exhausted, they die. The sulfuric acid formed as a result of the oxidation of the sulfur is neutralized by calcium carbonate or bicarbonate present in the water. The energy obtained from the oxidation is utilized for the assimilation of carbon dioxide. For every gram of carbon synthetized, about 8 to 19 grams of sulfur are consumed.

A large heterogeneous group of bacteria which do not form filaments also oxidizes hydrogen sulfide and accumulates granules of sulfur within the cells. Another group oxidizes hydrogen sulfide and thiosulfate with the production of sulfur not within but outside their cells. A group of minute non-filamentous forms oxidizes elementary sulfur with the formation of sulfuric acid.

A very interesting group of sulfur bacteria, known as the purple bacteria, contains a red pigment (bacteriopurpurin) and a green pigment (bacteriochlorin). The red pigment absorbs light from the red end of the spectrum. While the physiology of these bacteria is not well understood and important points are in question, it is generally believed that they have some sort of photosynthetical process, although they may not be able to make extensive use of it. These bacteria may show an indication of the beginning of some such photosynthetical process as is found in green plants.

Nitrite and nitrate bacteria. A large amount of ammonia is produced by the decay of animal and plant materials, ammonia being the chief nitrogenous end-product of their decomposition. A group of organisms known as nitrite bacteria obtain energy for the synthesis of carbon from the oxidation of ammonia with the production of nitrites. Another bacterium obtains energy through the oxidation of nitrites to produce nitrates. The nitrite and nitrate bacteria are not only interesting on account of their method of obtaining energy, but are exceedingly important for soil fertility in that they conserve the nitrogen of decaying organic material and convert it into the form in which it is most usually absorbed by higher plants. They are present in all soils except very acid ones.

The commonest nitrite bacteria belong to the genus *Nitrosomonas*, of which there appear to be various forms in different parts of the world. *Nitrosomonas* is oblong or rounded, and, when motile, has a single flagellum. The other genus of nitrite bacteria is *Nitrosococcus*, which is a non-motile coccus form. The nitrate bacterium is *Nitrobacter*, a non-motile rod-shaped bacterium.

Bacteria oxidizing iron. The nitrifying bacteria are strictly autotrophic. Some of the sulfur bacteria can utilize organic compounds. This is still truer of the iron bacteria; while there is much difference of opinion as to the physiology of the group, it appears that some can oxidize ferrous to ferric iron and use the energy thus set loose for the assimilation of carbon.

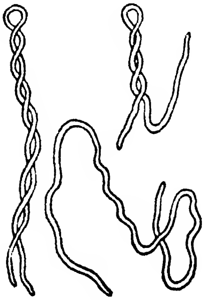


FIG. 416. *Gallionella ferruginea*, an iron bacterium

After Migula

Probably some (*Spirophyllum*) cannot live without ferrous bicarbonate, while others (*Leptothrix*) can live without it, or, if it is present, can utilize it. Still other bacteria accumulate iron by purely mechanical means and are not true iron bacteria. Some iron bacteria (*Leptothrix* but not *Spirophyllum*) can utilize manganese bicarbonate in place of ferrous bicarbonate.

Bacteria oxidizing other substances. One bacterium (*Micrococcus selenicus*) can obtain energy by the oxidation of selenium compounds, a number can oxidize hydrogen to water, others oxidize methane, while some other hydrocarbons and also carbon monoxide can be utilized by certain bacteria.

Heterotrophic bacteria. Bacteria which can utilize carbon only when it is in the form of organic compounds are said to be heterotrophic. Such bacteria are necessarily dependent on other organisms for the production of organic carbon compounds. Heterotrophic bacteria, therefore, are either parasitic, obtaining their carbon from living organisms, or saprophytic, getting carbon from the dead remains or the dead products of living organisms.

Nitrogen-fixing bacteria. These bacteria are heterotrophic, and so need carbon in organic form. They can ordinarily, however, obtain the nitrogen they need from the uncombined nitrogen of the atmosphere, while most plants require nitrogen in the form of compounds. Among the nitrogen-fixing bacteria there are a number of widespread forms that live free in soil, and a type that occurs in nodules on higher plants, chiefly on the roots of legumes, such as beans, peas, clover, and alfalfa. These bacteria are exceedingly important from the standpoint of soil fertility, as they may supply large amounts of nitrogen to the soil. Nitrogen is essential for the building of proteins, and it is the element in which soils are most likely to be lacking. Some combined nitrogen is added to the soil as the result of electrical discharges in the atmosphere, but the amount is very small as compared with that resulting from the activities of nitrogen-fixing bacteria. Before the action of nitrogen-fixing bacteria was known, some scientists thought that the exhaustion of the supply of combined nitrogen would result in the end of civilization. The activity of the bacteria in the nodules on the roots of legumes explains the value of legumes in enriching the soil.

Free-living nitrogen-fixing bacteria. Nitrogen fixation is due to both *anaerobic* and *aerobic* bacteria. The first can grow in the absence of oxygen, and in some cases cannot grow if more than a very small amount is present; the latter require oxygen. The best-known anaerobic nitrogen-fixing form is *Bacillus* (*Clostridium*) *amylobacter*. The most important aerobic ones belong to the genus *Azotobacter*, which is rod-shaped and flagellated. The fixation of nitrogen requires energy. This is furnished by organic carbon compounds which are oxidized by the nitrogen-fixing bacteria. The fixation of nitrogen may be increased when *Azotobacter* is associated with certain other bacteria. Thus, bacteria which act on cellulose may furnish carbohydrate material which *Azotobacter* can utilize as a source of energy for the fixation of nitrogen. Again, there may be a sort of symbiosis with an anaerobic form such as *Bacillus amylobacter*; *Azotobacter* uses up the oxygen and makes conditions favorable for the anaerobic form, and this in turn produces organic acids which, after being neutralized in the soil, can be utilized by *Azotobacter*. Various other complexities occur. In general, nitrogen-fixation is most rapid in light, well-aerated soils supplied with enough humus to furnish a sufficient source of energy.

Symbiotic nitrogen-fixing bacteria. The invasion of the roots of legumes by *Bacillus radicicola* (Fig. 417) results in the formation of nodules on the roots (Fig. 384). *Bacillus radicicola* multiplies in these and fixes atmospheric nitrogen, apparently in greater quantities than are required by the bacteria; at least the leguminous plants with bacterial nodules contain more nitrogen, and in general are more flourishing, than the same kinds of plants without nodules. When the legumes die and they with the nodules are decomposed, nitrogen is added to the soil. Owing to these facts, soils may be enriched with nitrogen by the growing of leguminous crops. For this reason it is often desirable to alternate non-leguminous and leguminous crops, so that the fixation of nitrogen by the bacteria in the roots of the legumes may make up, at least in part, for the nitrogen removed by the non-leguminous crop.

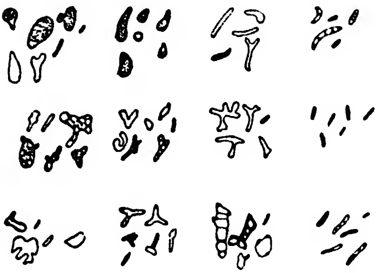


FIG. 417. *Bacillus radicicola* from various plants

After Buchanan

The bacteria come in contact with a root hair and form small clumps, the part of the wall of the hair in contact with the bacteria softens, and the bacteria then enter the hair. They multiply rapidly and, in the form of threads or strands, advance through cells and walls. In older nodules they become arranged as slimy masses around the vacuoles of the cells.

Bacillus radicicola occurs in several forms, including normal rods, oval swarmers, and irregular-shaped and branching vacuolated bodies (*bacteroids*). In young nodules the rods and oval forms predominate, while in old decomposing nodules there are mostly extremely vacuolated, branched forms.

Strains of *Bacillus radicicola*. Some strains of *Bacillus radicicola* have flagella all around them, while in others they are found only at one end.

Experiments indicate that there are also a number of strains which differ from each other physiologically although they cannot be distinguished morphologically. Thus, a bacterium isolated from one leguminous species will cause the production of nodules only on other plants of that species or of that species and certain others. As a number of such physiological strains have been isolated, it is apparent that it is necessary to use the right strain in order to produce nodules on a given legume.

Denitrification. Some bacteria reduce nitrates with the production of nitrogen gas, which escapes into the air. For this reduction most of the denitrifying bacteria utilize organic carbon compounds as a source of energy. For rapid denitrification, these bacteria, which are anaerobic, require the complete or almost complete absence of oxygen, and a considerable supply of carbohydrates and nitrates. Such conditions are found in heavy soils saturated with water and rich in humus.

Decay bacteria. The remains of plants and animals do not decay by themselves, but are destroyed by the action of other organisms; and in this process bacteria play a most important part. We know that fruit and meat decay very rapidly if no care is taken to prevent this process. That the decay is not due to anything inherent in the substances themselves is shown by the process of canning, as when we sterilize milk, meat, or fruit by heat and then seal them in cans. The reason that these substances do not decay under such conditions is that by heating we kill all the living organisms that would destroy them, while by sealing we prevent the access of other organisms. Decay can also be prevented by the use of poisons which make the life activities of organisms impossible. Use is made of this fact in treating timber with creosote or other poisonous substances, the wood being preserved so long as sufficient poison is present. In fact, any set of conditions which prevents the growth of living organisms serves to preserve organic matter. The keeping qualities of foods preserved in concentrated sugar or salt are due to the high osmotic pressure, which tends to result in the plasmolysis of the cells of bacteria or molds which might cause the spoilage of the food.

In the destruction of organic matter a great variety of organisms take part. They include all animals, as well as the heterotrophic bacteria, fungi, and other saprophytic and parasitic plants. That part of the destruction which we usually regard as decay is due largely to bacteria and fungi, bacteria playing a most important part.

Importance of decomposition. Decay of dead organic material is very necessary for the continuance of life. In the growth of green plants and of animals, large quantities of important chemical elements are stored up in organic compounds. When plants or animals die, the elements in these organic compounds are not immediately available to green plants but must first be reduced to simple inorganic compounds. In causing the decay of organic remains and thus returning the elements to the soil in a form in which they are available to higher plants, the bacteria perform a very useful function. If it were not for the action of organisms which cause decay, it is reasonable to suppose that the earth would be deeply covered by the products of the life activities of the higher organisms, and in these products would be stored carbon and nitrogen necessary for the growth of living things.

When bacteria cause the decay of substances such as wood or food which man desires to preserve, they are regarded as injurious. It should be noted, however, that in causing decay the bacteria perform a function that is naturally very useful.

Process of decomposition. Decay is not due to any one bacterium but to a great number. The breaking down of complex compounds takes place in successive stages, and different types of compounds are acted on by different series of bacteria. Among the most important of the series of decay bacteria are those which act on cellulose and return the carbon to the air in the form of carbon dioxide, and those which utilize protein and its decomposition products with the ultimate production of ammonia, which is converted by nitrifying bacteria (nitrite and nitrate) into nitrates that are available to green plants.

Decomposition of cellulose by soil bacteria. A short description of the decomposition of cellulose will serve to give an idea of decomposition in general. A variety of different bacteria act on cellulose in the soil, the series of bacteria varying with environmental conditions. This decomposition is brought about by enzymes just as is other organic decomposition and digestion in general. The enzymes are secreted or excreted by the bacteria. Under favorable conditions the cellulose is hydrolyzed to the disaccharide *cellobiose* by the enzyme *cellulase.* The enzyme *cellobiase* then changes the cellobiose to glucose. This is decomposed by a variety of organisms to form various organic acids, which in turn are broken down to form carbon dioxide and water.

The initiation of the digestion of cellulose in the alimentary canal of herbivorous animals is due to the activity of bacteria. The herbivorous animals are like human beings in that in themselves they cannot digest cellulose. Enzymes excreted by the bacteria, however, change the cellulose to sugars which can be digested by the animals.

Decomposition of cellulose and the carbon cycle. The carbon which plants absorb from the air in the form of carbon dioxide, and assimilate through photosynthesis, is stored in various organic compounds; to a considerable extent, in cellulose. Bacteria which break down cellulose and other organic compounds with the production of carbon dioxide return some carbon to the air. The plants and the bacteria produce what we may think of as a carbon cycle, the plants building up the carbon into complex compounds, and the bacteria returning it again to the atmosphere in the form of carbon dioxide. The bacteria are, of course, not the only agents which return carbon to the atmosphere. Green plants themselves through respiration do so. All animals and all parasitic and saprophytic plants do the same. Carbon dioxide is also produced by the burning of organic compounds. Thus, in the carbon cycle, the carbon which is assimilated by green plants may be returned to the atmosphere by various agents. The atom of carbon may easily take part in the metabolism of various organisms before it finally reaches the air again, as it may pass from plants through various animals and finally be made into carbon dioxide by bacteria.

Decomposition of proteins and the nitrogen cycle. There are many proteins, and they are decomposed by a large number of bacteria, some of which act on the proteins while others only utilize the decomposition products. The ultimate result is the production of ammonia, which is converted first to nitrites and then to nitrates by the nitrifying bacteria. The nitrogen is then in its most suitable form for use by green plants, by which it is employed in the synthesis of proteins. The nitrogen of organic matter thus goes through a cycle which, expressed in very simple terms and without complications, is from nitrates to proteins in green plants, to ammonia through decomposition of protein, and back to nitrates through the activity of the nitrifying bacteria. There are, as we have seen, various complications in this cycle. Some nitrogen is lost to the atmosphere in the breaking down of proteins and some through the activities of denitrifying bacteria, while nitrogen enters the cycle by the work of nitrogen-fixing bacteria. As the proteins of green plants may be reworked by animals and other organisms a number of times, any atom of nitrogen may be present in the protein of many different organisms before it forms a part of a simple decomposition product.

BACTERIA AND DISEASE

Pathogenic bacteria. Many bacteria live within the body of an animal (that is, in the cavities opening to the exterior and on the mucous membranes) without usually doing visible harm. Under special conditions, as when the resistance of the host is lowered, some of them may become pathogenic. There are, however, numerous bacteria which are very pathogenic for a particular host or group of hosts and which are extremely important as causal agents of infectious and contagious diseases. The influence of bacteria in causing human disease is so well known that many people think of bacteria in this connection only, and neglect the fact, if they ever knew it, that bacteria as a class are much more beneficial than harmful.

Causes of diseases. Some infectious diseases, as malaria, may be due to small animals; others, as smallpox, are caused by filterable viruses, which are bodies so small that they cannot be seen with a microscope and will pass through the finest filter; still others are produced by fungi. However, the majority of communicable human diseases are the result of bacterial action. These include such well-known scourges as tuberculosis, leprosy, plague, cholera, typhoid fever, pneumonia, diphtheria, tetanus, anthrax, dysentery, and meningitis. Bacteria are also responsible for many diseases of animals. Plant diseases are more largely due to fungi, but many are bacterial.

Infectivity of bacteria. Most of the highly pathogenic bacteria naturally infect only one host or a group of more or less closely related hosts. It is, however, often possible to infect an animal artificially with bacteria which do not naturally attack it. Pathogenic bacteria ordinarily live as parasites, but most of them can live saprophytically, as is evident by the ease with which they can be grown in test tubes on artificial culture media. In some cases it has not been possible to grow bacteria thus, but this may only mean that the proper conditions for such growth have not been found.

The leprosy bacillus is a good example of a bacillus confined to one host. This bacillus occurs naturally only in man. The only artificial infections in animals were produced in monkeys with difficulty, and healed without treatment. There have been claims that the bacillus has been grown on artificial media, but there is no proof that it can be thus grown continuously.

Immunity. A plant or an animal which does not take or cannot be given a disease is said to be immune to that disease. Organisms which produce plant diseases do not grow on animals; so animals are immune to such organisms and the diseases which they produce. Similarly, man is immune to most animal diseases. Immunity may be due to various factors, some of which are relatively simple. It is not surprising that bacteria may be pathogenic for warm-blooded animals and not for cold-blooded ones, and vice versa. Tetanus does not affect frogs under ordinary conditions, but may do so if the temperature is raised artificially. The acidity in the dog's stomach is high enough to kill the bacteria that cause intestinal diseases in man. The above examples show that pathogenic bacteria require suitable conditions for growth.

The portal of entry of bacteria into the body is important from the standpoint of the production of disease. The tetanus bacillus is found in the intestinal tracts of a considerable proportion of men, and is still more prevalent in the intestines of horses and cattle, which seem to be its normal habitat. However, it may produce fatal infection if introduced into deep wounds of either men, horses, or cattle. Conversely, the typhoid bacillus, which is often fatal in the intestinal tract of man, produces only a slight and largely local reaction if injected subcutaneously.

Not only is man immune to most of the bacterial diseases of animals, but an individual may have more or less natural or acquired immunity to a given human disease. At times this immunity is sufficient to resist a slight but not a heavy infection. The relative immunity of an individual to an organism pathogenic for the race is a very complicated subject. Moreover, it is largely a question of the reaction of the animal body. A lengthy discussion would therefore be out of place in a textbook of botany, and so only a very short account will be given.

The destruction of bacteria in the body seems to be due largely either to the action of the cells (chiefly white blood cells) which ingest and destroy the bacteria (*phagocytosis*) or to the bactericidal action of the body fluids, most often the fluid part of the blood.

This bactericidal action is due to substances known as antibodies, which may be naturally or artificially acquired. The term *antibody* is a very inclusive one and embraces a variety of different substances. It is used for convenience rather than for exactness.

Acquired immunity. It is well known that when a person has recovered from any one of a number of infectious diseases, he has acquired an immunity to that disease. The immunity is due to the production by the body of antibodies which react against the causal agent of the disease or neutralize its toxin. The amount of antibodies produced depends on the inciting stimulants of bacterial cells or toxins and on the body response. The antibodies remain for a short or a long time in the body, thus giving a temporary or a permanent immunity. Antibodies can be artificially produced by the injection into the body of dead bacteria or their toxic products, a process which is used extensively in vaccinating against bacterial diseases such as typhoid fever and cholera.

A few bacteria, such as the diphtheria and tetanus bacilli, produce violent specific poisons (*toxins*) in the media in which they grow. When these toxins are injected in increasing doses into the body of an animal, the tissues are stimulated to produce antibodies, known as *antitoxins*, which can neutralize the toxins which led to their production. Antitoxins produced in one animal can be injected into another to neutralize toxins in the second, as when diphtheria antitoxin from the blood serum of a horse that has been immunized with diphtheria toxin is used to cure diphtheria in a human being.

BACTERIA IN INDUSTRY

Bacteria are very important industrially because of their destruction of food and other products and the trouble which is necessary to prevent damage by them. But some are of value in various industries because of chemical changes which they produce.

Since the days of ancient Egypt, bacteria have been employed, even though unconsciously, in the retting of flax, the fiber from which linen is made. The flax fiber is the bast fiber in the bark. In retting, the plants are either immersed in water or exposed to dew and rain, when bacterial fermentation loosens the bark from the wood, and the fiber from surrounding tissue.

Alcohol results from the fermentation of sugar by the yeast fungus. Acetic-acid bacteria, of which there are a number of different species, ferment alcohol with the production of acetic acid. The result is vinegar, which is essentially a solution of acetic acid plus aromatic and flavoring substances. Natural vinegar is made from wine, apple cider, and various other materials. Synthetic vinegar is prepared by diluting chemically manufactured acetic acid, often with the addition of coloring material.

Sauerkraut is the result of bacterial fermentation of cabbage. The cabbage is sliced and packed in alternate layers with salt. This results in the withdrawal of water from the cabbage. The fermentation of the juice produces acids, largely lactic acid, which prevents the development of putrefying bacteria. Oxygen is excluded to prevent the growth of molds and other organisms which might destroy the acids.

The preservation of silage is due to a lactic-acid fermentation by bacteria, similar to that in the case of sauerkraut.

Souring of milk is caused by various lactic-acid bacteria. The sour taste of buttermilk is due to lactic acid. Much so-called buttermilk is now made by adding bacteria to milk. In the manufacture of butter bacteria play a prominent part, because in the ripening of the cream they have great influence on the flavor. In much modern practice, desirable lactic-acid bacteria are added to the cream to produce a uniform good flavor. The characteristics of a number of important types of cheese are connected with bacterial action.

RELATIONSHIP OF BACTERIA

Bacteria are simple organisms. The question of the place of bacteria in the plant kingdom is most interesting. When an organism has a simple structure, it is necessary to inquire whether the simplicity is due to primitiveness or whether it has resulted from the simplification of a more complex structure. There are reasons for thinking that bacteria are very ancient and primitive.

No fossils are definitely recognized from the oldest geological era, the Archeozoic, but immense graphite deposits indicate the presence of organisms, the remains of which were decomposed by the action of bacteria. While there is little evidence as to the exact nature of these organisms, they must have been very primitive. Also the presence of bacteria in this era is inferred from the occurrence of iron ore and limestone believed to have been formed by bacterial action. There are reasons to believe that in Proterozoic times bacteria were present and widespread. Bacteria resembling living iron bacteria have been found in connection with iron ores of this era.

Bacteria are ancient. Geological evidence thus indicates that bacteria are as ancient as any other known plants, if not more so. Of course there may have been more primitive and ancient organisms of which we have no knowledge. The visible structure of bacteria is the most primitive of which we know, and this is what might be expected in an ancient and primitively simple group. It is only among the bacteria that we find methods of nutrition that could have enabled an organism to live on inorganic materials before the evolution of chlorophyll and photosynthesis. The nutrition of most groups of plants is comparatively uniform, but among bacteria there is great diversity. This indicates an ancient stock, as this diversity must have necessitated a long evolutionary history. Also, considering the simplicity and small size of the bacteria, there is great variety in form of both individuals and colonies.

Advantage of small size. The small size of bacteria affords a very evident advantage; for the smaller the size of a cell, the greater, in comparison with the bulk of the cell, is the surface available for the exchange of materials with the outside. The bacteria have retained the advantage afforded by small size, but have developed along many diversified lines. This tendency toward development in various directions is characteristic of all great groups of living organisms.

Some bacteria of recent origin. While the bacteria as a group appear to be very primitive, it does not follow that all individual species are ancient. Indeed, those that naturally live only in the human body would appear to be of relatively recent origin, as they have physiological properties which they could hardly have acquired before the advent of man or of animals rather closely related to him.

CHAPTER XVIII

SCHIZOPHYTA

CYANOPHYCEAE: BLUE-GREEN ALGAE

General characteristics. The blue-green algae belong with the bacteria in the division or subdivision *Schizophyta.* They resemble the bacteria in their method of cell division and in the absence of sexual reproduction. They are a most interesting group because they are the simplest plants with chlorophyll and they have a central body or incipient nucleus which may be regarded as being intermediate in structure between the nuclei of higher plants and the granules staining like chromatin which are found in the bacteria. They consist of single cells, filaments (rows of cells), or colonies in which either individual cells or filaments are held together in gelatinous masses (Figs. 418–421). Reproduction is always, as in the bacteria, asexual, and is most usually due to cell division or the fragmentation of colonies or filaments. The popular name "blue-green algae" refers to the characteristic blue-green color of the great majority of these plants. The color is due to a combination of the green pigment chlorophyll and a blue pigment, phycocyanin. They also contain the yellow pigments which are associated with chlorophyll, while a red pigment is found in many of them. In some members of the class various combinations of these pigments give them colors which are very different from the typical blue-green. Thus the Red Sea has been said to have got its name from a floating red one which is occasionally present in such quantities as to impart its color to the water. The blue-green algae do not have plastids; the pigment is diffused in the protoplasm, usually in the peripheral portion of the cell. The absence of plastids and the diffused blue-green color serve to distinguish the blue-green algae from other plants when viewed under a microscope. With the unaided eye they can usually be recognized by the combination of their blue-green color and slimy appearance.

The gelatinous material so characteristic of most blue-green algae is derived from the swelling of the outer parts of the cell walls. Often the gelatinous covering of the cells appears to be in layers, which, in some colonial forms, makes it possible to identify the sheaths of successive cell generations (Fig. 419). In other cases there is no such distinction and the cells appear to be distributed in a continuous transparent gelatinous mass (Fig. 423). In many filamentous forms the gelatinous material forms a conspicuous sheath (Fig. 422). In other cases the sheaths of different filaments are confluent, so that many filaments appear to be embedded in a homogeneous matrix. The gelatinous material consists largely of pectic compounds, but cellulose may be present. In some forms the sheath is only slightly developed or absent.

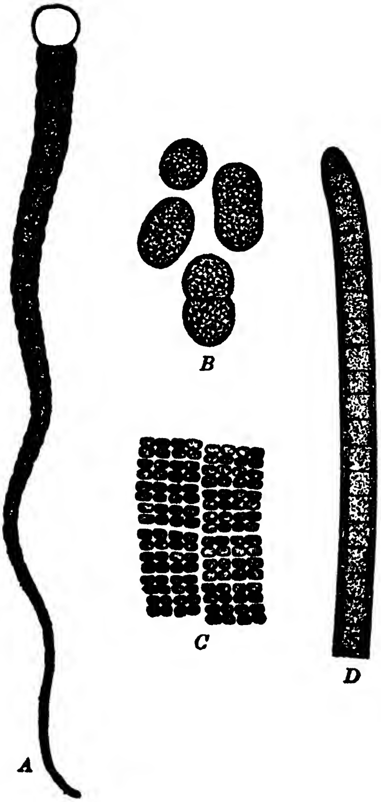


Fig. 418. Forms of blue-green algae

A, Rivularia; *B, Aphanothece*; *C, Merismopedia*; *D, Oscillatoria*

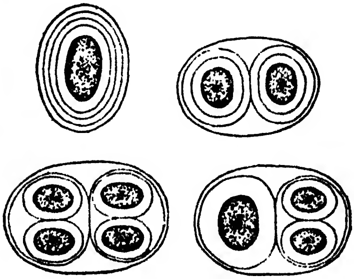


Fig. 419. ***Gloeocapsa***

A single-celled individual and colonies of two, three, and four cells. (× 1285)

Form of colonies. In most colonial forms the cells divide in three planes and are scattered irregularly in the matrix. Such colonies are usually without special shape. In a few genera the cells have a regular arrangement in a definitely shaped colony. In *Merismopedia* the cells divide in only two planes, and as a result the colony is a rectangular plate (Fig. 418). In some other cases division in only two planes leads to the production of hollow spherical colonies in which the cells form a single layer near the periphery of the mucilaginous matrix that holds the colony together (Fig. 423). Other interesting forms are shown in Figs. 424–427.

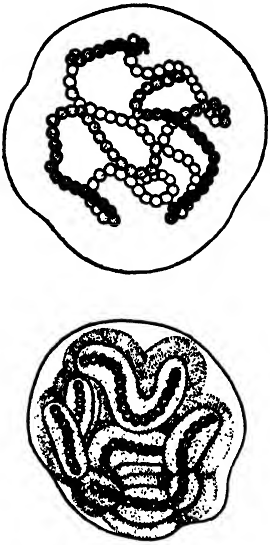


FIG. 420. Two species of *Nostoc*, each embedded in a gelatinous matrix

Cell structure. The cells of the blue-green algae are characterized by having a colorless central portion, the so-called *central body*, surrounded by an exterior portion in which the pigment is diffused. The central body seems to represent an incipient nucleus. However, it is not separated from the rest of the cell by a membrane; it has no nucleolus; it does not divide mitotically, at least not by such a complicated and clear-cut process as in higher plants; and its structure, while showing a good deal of variation, is always much more primitive than that of an ordinary nucleus. In forms which show what may be regarded as the most primitive condition, there appears to be no distinction between the protoplasm of the external and central portions of the cell except that granules which seem to be chromatin are scattered in the central region. In the more specialized forms there is a very clear differentiation between the central body or incipient nucleus and the surrounding protoplasm, even though there is no separating membrane (Figs. 428–430). In such cases the central body may show a chromatin reticulum which is very suggestive of that of the nucleus of higher plants.

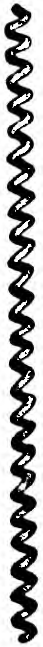


FIG. 421. A filament of *Spirulina*, a blue-green alga. (× 925)

The division of the protoplasm is generally accomplished by the growth of a wall which starts as a ring formed on the wall of the mother cell and grows inward (Fig. 428). In some cases the chromatin material divides ahead of the ingrowth of the wall (Figs. 429, 430); in others it appears as though it were divided by the growth of the wall.

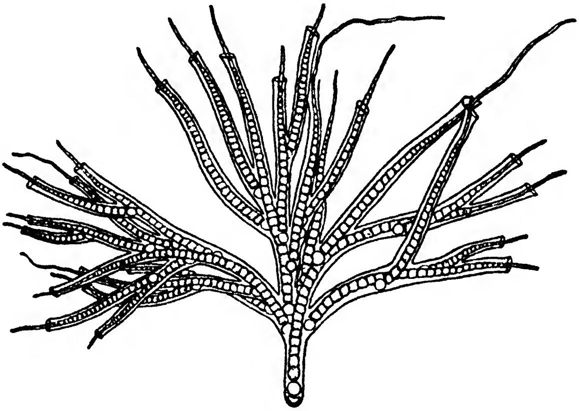


Fig. 422. ***Rivularia mammillata***

After Setchell

When the cells of the blue-green algae are viewed under the microscope they often show granules or globules. Those in the outer region are known as cyanophycin granules, while those in the incipient nucleus are designated slime globules. Both seem to be albuminous reserve material.

Sugar and glycogen, often called animal starch, are found in the cells. The glycogen, which is commonly present in animal tissue but rare in plants, appears to take the place of starch, which is not found in the blue-green algae. Frequently oil globules occur in the cells.

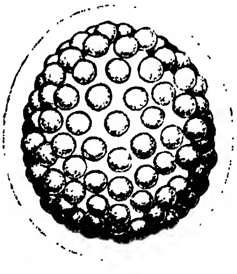


Fig. 423. ***Coelastrum*, a colonial blue-green alga in which cells are arranged in the form of a hollow sphere embedded in a gelatinous matrix. (× 400)**

In those species of blue-green algae in which the plant consists of an individual cell or a colony of cells held together by mucilaginous material all the cells are alike. In many filamentous forms all cells are alike except that the end cell is convex on the side where it is not pressed by a neighboring

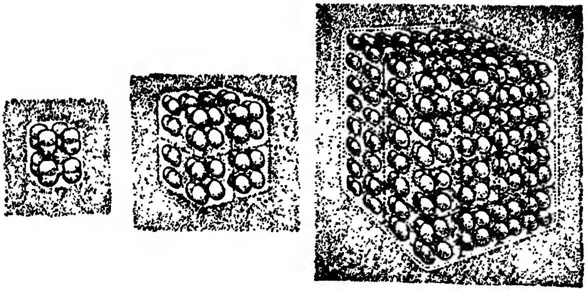


Fig. 424. *Eucapsis alpina*, a blue-green alga which divides in two planes and forms cubical colonies embedded in a gelatinous matrix

After Clements and Shantz

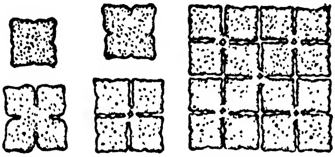


Fig. 425. *Tetrapedia gothica*

A single cell and its development into a plate of sixteen cells. (× 625). After Reinsch

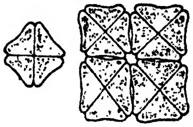


Fig. 426. *Tetrapedia emarginata*

Four-celled and sixteen-celled colonies. (After Schröder)

cell. In one group of filamentous blue-green algae the cells of a filament taper markedly toward one (Fig. 422) or both ends. In the majority of filamentous genera there are special cells known as heterocysts (Figs. 431, 432) which occur either in or at the ends of the filaments. These are usually enlarged cells with thickened walls.

Heterocysts develop from ordinary cells, and generally lose their pigment and become yellowish as the cell wall thickens. For a considerable time they are connected with the adjoining cells by pores which extend through conspicuous thickenings at the ends of the cells. When the heter-

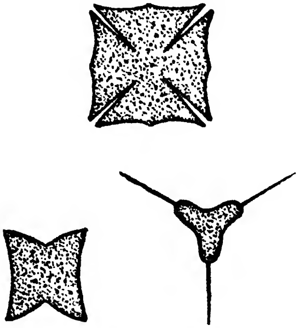


Fig. 427. Three peculiar types of blue-green algae

At top, *Tetrapedia crux-michaeli*; lower left, *Tetrapedia reinschiana*; lower right, *Tetrapedia setigera.* (After Ascher)

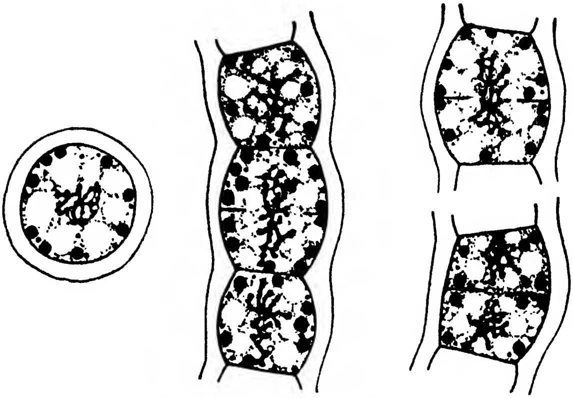


Fig. 428. *Anabaena circinalis*

Left, a cross section of a cell; center, a longitudinal section of three cells the middle one of which is dividing; right, longitudinal sections of two individual cells in stages of division. The deeply staining threads near the centers of the cells stain like chromatin. (× 2000). From Haupt

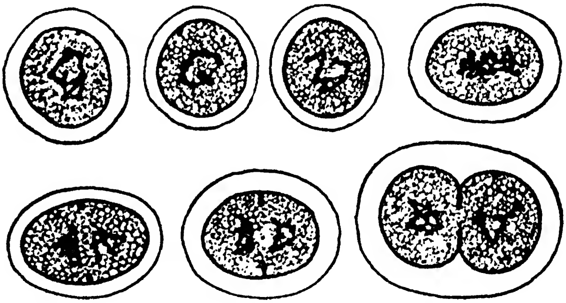


Fig. 429. *Gloeocapsa aeruginosa*

The first three upper figures are sections of cells not in division. The remaining figures show sections of dividing cells in successive stages of division. The deeply staining threads near the centers of the cells stain like chromatin. (× 2000). After Haupt

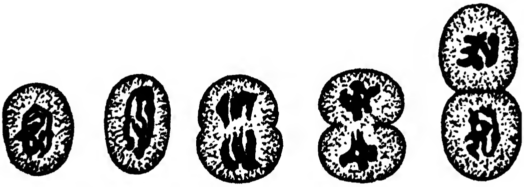


Fig. 430. *Synechocystis aquatilis*

A resting cell and several stages of division. (After Gardner) ocysts are terminal there is no thickening or pore at the free end. Finally the protoplasmic contents degenerate and vanish.

Branching. Some of the filamentous blue-green algae do not branch, others have true branches which are lateral outgrowths of the filament, while still others are characterized by "false" branching. In forms with true branching the filament often consists of more than a single row of cells. In false branching the filament becomes ruptured and either one or both of the ends thus formed push out of the side of the sheath (Figs. 433, 434). In forms with single "false" branches there is often a heterocyst just above the point where the branching occurs. When there are paired branches, heterocysts are not found at the point of rupture.

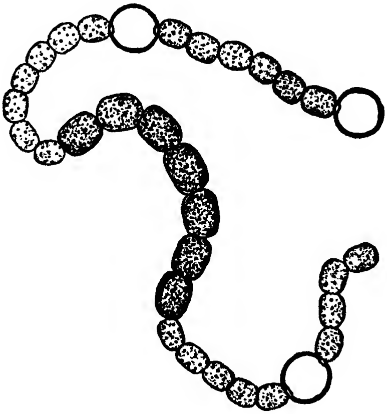


Fig. 431. *Nostoc*

A filament with three heterocysts (the large rounded cells which appear empty) and seven resting spores (the large cells near the center of the filament)

Reproduction. Unicellular blue-green algae multiply only by cell division. This is the simplest method of reproduction known and shows no advance over that of the bacteria. The general method in colonial forms is the division of cells to form colonies and the fragmentation of these into smaller colonies after they have attained some size.

Reproduction in filamentous forms is due mostly to the division of filaments to form short lengths called hormogonia. In some forms heterocysts occur at the points of rupture. However, in forms both with and without heterocysts, the formation of hormogonia may be independent of heterocysts. In some cases fragmentation is due to the secretion at intervals in the filament of a substance between adjacent cells. This forms biconcave separation discs which are at first green but may become colorless. In other cases the formation of hormogonia results from the dying of a cell which is first compressed by neighboring cells and then disintegrates (Fig. 435).

Some of the filamentous forms reproduce by means of resting spores. These are formed from ordinary vegetative cells which, usually enlarging, become densely filled with food material and have their contents surrounded by two distinct cell membranes (Fig. 431). These resting spores may remain dormant for a long time and are resistant to unfavorable conditions. They thus serve not only for reproduction but also for continued existence under adverse conditions which might be fatal to vegetative cells. When the spore germinates, the spore membranes become ruptured and the contents divide to form a filament of cells (Figs. 436, 437).

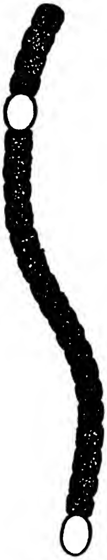


FIG. 432. *Anabaena* with heterocysts. (× 535)

The division of the protoplast may start either before or after the rupture of the spore covering. This rupture may be due either to a dissolution of a small part of the membrane or to its separation. Among the solitary and colonial forms resting spores are known only in one genus, *Gloeocapsa.*

Reproduction by gonidia is characteristic of the small and relatively unimportant order *Chamaesiphonales.* The plants of this order are always attached to some object, and consist of either single cells or a cushion formed of creeping, attaching filaments with upright branches. The inner part of the cushion may become gelatinous so that its filamentous nature is obscure. The contents of large terminal cells divide to form numerous small rounded reproductive cells, the gonidia (Figs. 438, 439). In these plants there is a differentiation between cells which remain permanently vegetative and others which become reproductive. Gonidia formed singly in vegetative cells have been reported in a few of the more usual filamentous types.

Movement. All hormogonia have a slow motion, some in a straight line, others in a spiral. This movement may carry them away from the site of their formation. Some mature filaments have a similar movement. This is very marked in *Oscillatoria* (Fig. 418), the name of which refers to its oscillations. The filaments glide forward and backward and rotate while the tips swing to one side or the other. *Spirulina* (Fig. 421) moves through the water with a corkscrew motion. The mechanism of these movements is not understood. Flagella or other organs of locomotion are not known among the blue-green algae.

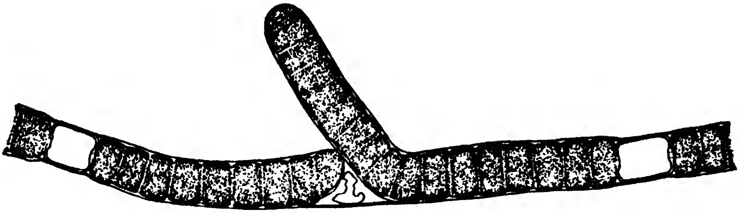


FIG. 433. *Tolypothrix* showing two heterocysts and false branching
Note remains of a dead cell where branching occurred. (× 415)

Distribution. The *Cyanophyceae* are found in all parts of the world. They usually occur in water or in damp localities, but also occur in dry situations. They are frequently very abundant in fresh water, and sometimes occur in such quantities as to produce a distinct color, the so-called "waterbloom." The *Cyanophyceae* may have an unpleasant odor, and when they occur in water in great quantities, their death and decay frequently gives the water a very disagreeable odor and taste. In this way they may become a great nuisance in water supplies or to people living along bodies of water

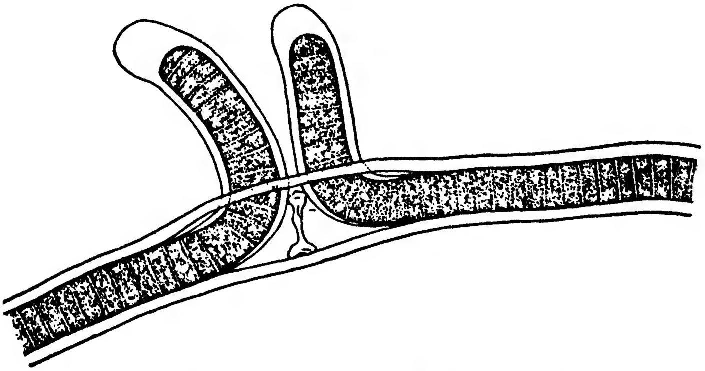


FIG. 434. *Scytonema* showing false branching

in which they are too plentiful. They may be responsible for the death of fish or even cattle. Some blue-green algae can withstand higher temperatures than other algae and are abundant in hot springs. A lichen is a combination of a fungus and an alga; blue-green algae frequently furnish the algal component.

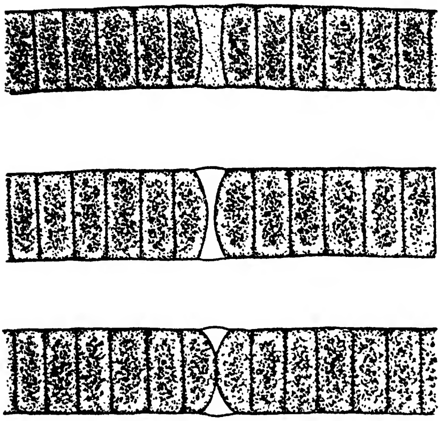


FIG. 435. *Oscillatoria*, showing stages in division of a filament by death of a cell

Representative forms. *Gloeocapsa* (Fig. 419) is a very common blue-green alga that occurs as single cells or groups of two to eight or more rounded cells held together by the gelatinous cell walls. Each cell has its own sheath, and two cells may be held together by the sheath of the mother cell. Likewise the sheaths of two such mother cells may be surrounded by the sheath of the grandmother cell. It is in this way that the groups are formed. Reproduction is by cell division.

In *Merismopedia* (Fig. 418), as in *Gloeocapsa*, the cells are held together by a gelatinous matrix. However, division of the cells takes place alternately in two planes perpendicular to each other, so that the colony takes the form of a flat plate. Reproduction is by cell division and the fragmentation of the colony.

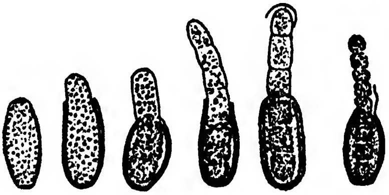


FIG. 436. A resting spore of *Anabaena* and stages in its germination. (× 330)

After Thuret

Oscillatoria (Fig. 418) can be recognized as a naked filament composed of flattened cells and with a very characteristic oscillating movement. Reproduction is usually by the formation of hormogonia due to the occurrence of dead cells or separation discs. No heterocysts are known.

Nostoc (Figs. 420, 431) is characterized by twisted filaments of more or less rounded cells, conspicuous round heterocysts, and the frequent occurrence of rows of large resting spores. The sheaths of the individual filaments are distinct (Fig. 420) in some cases, while in others they are so coalesced and transparent as to be invisible (Fig. 420).

Blue-green algae are primitive. The apparently simple structure of the cell of the *Cyanophyceae* and the absence of a sexual method of reproduction indicate that they are very primitive forms of plants. The bacteria, which lack chlorophyll, are the only other plants that do not have definite nuclei, while the *Cyanophyceae* are the only plants with chlorophyll that do not have chloroplasts. For these reasons the *Cyanophyceae* are regarded as the most primitive chlorophyll-bearing plants.

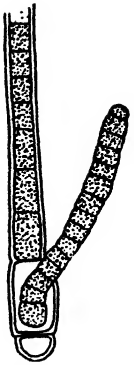


Fig. 437. A spore of *Calothrix fusca* which has germinated to produce a filament while still attached in the filament in which it is formed

After Teodoresco

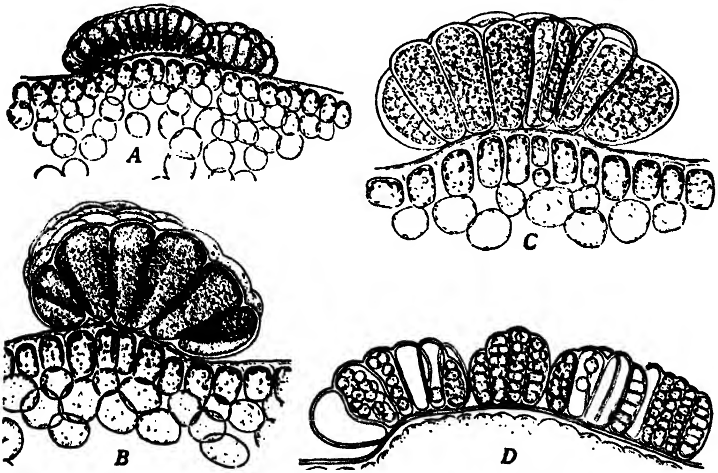


Fig. 438. *Dermocarpa prasina*, a blue-green alga which produces gonidia

The illustration shows growth of a colony and the formation of gonidia. The rather loose cells which are below the *Dermocarpa* are a part of the plant on which the *Dermocarpa* was growing. (× 500). After Bornet and Thuret

There are reasons to believe that in Proterozoic times blue-green algae (*Cyanophyceae*) were present and widespread. Perhaps some of the blue-green algae were similar to living forms. The blue-green algae are such small and soft organisms that we should not, offhand, expect them to be readily fossilized. It is not surprising, therefore, to find that while there is evidence of this great antiquity, this evidence is rather circumstantial.

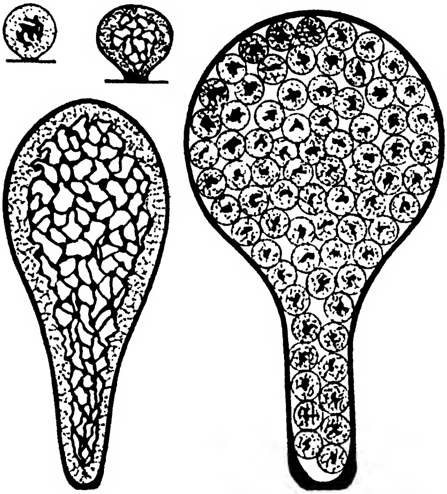


FIG. 439. *Dermocarpa fucicola*

Growth of individual and formation of gonidia as seen in section. (After Gardner)

Certain massive deposits of the Proterozoic era are regarded by eminent authorities as being due to blue-green algae. The algae would not have had to compete with higher plants, and there is little evidence of animals that ate them. Under these circumstances they would have had a much better chance to develop than at present. Both their presence and their abundance are inferred from the material believed to have been deposited around them, rather than from actual remains. At the present time "water biscuits," similar to the ancient deposits, are formed around blue-green algae by the deposition of calcium carbonate around the masses of algae and in the interstices within them (Fig. 440). It would seem that in Proterozoic times this same process built up deposits of limestone, and that the masses of blue-green algae were buried by an influx of ooze or mud that filled up the cavities and channels in the algal growth. The cavities in the deposits are interpreted as places formerly occupied by algae which have since disappeared. As various blue-green algae have different methods of growth, they would leave different and characteristic fossil impressions. Many such impressions have been described (Figs. 441–443). Microscopic examination of these deposits reveals what appear to be single cells, groups of cells, and chains of cells similar in shape to those of modern blue-green algae.

Fig. 440. Section of a calcium carbonate ball formed in connection with the growth of blue-green algae. (× ½)

After Walcott

Relationship of blue-green algae. It seems reasonable to suppose that the most primitive ancestors of the higher plants lacked a definite nucleus, and also that they did not have a method of sexual reproduction. Moreover, it would seem highly probable that the first plant that possessed chlorophyll did not have definite chloroplasts. It appears, therefore, that the *Cyanophyceae* possess many features that must have been characteristic of some of the primitive ancestors of the higher plants. Their primitive characteristics are in keeping with their apparent great antiquity. While there is no evidence that the *Cyanophyceae* themselves gave rise to the higher plants, it does seem probable that they and the higher plants had at least a common ancestor, and that in many respects the *Cyanophyceae* resemble this common ancestor very much more than higher plants do.

The only close relationship of the *Cyanophyceae* is to the bacteria, which they resemble in their method of cell division and in lacking sexuality and a highly organized nucleus.

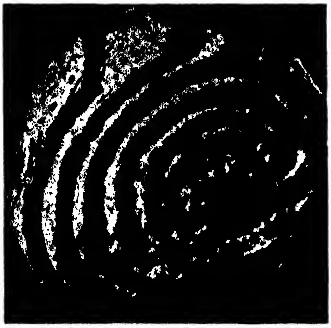


Fig. 441. *Newlandia concentrica*, a Proterozoic fossil believed to have been formed by the action of a blue-green alga. (× ¾)

After Walcott

The blue-green algae are not regarded as ancestral to the green algae because, among other reasons, it is believed that the latter are descended from a group of unicellular plants which move by means of flagella. In possessing flagella they resemble some bacteria more than they do the blue-green algae. Also they lack phycocyanin, so characteristic of the blue-green algae.

The blue-green algae show considerable morphological differentiation along various lines. This evolution was apparently independent of the varied lines of development of the bacteria, and shows no genetic relationship to the great diversification found in the algae. Thus we find in the blue-green algae the development of filaments; false and true branching; colonies in the shape of plates, hollow spheres, and cubes; heterocysts; rows of resting spores; hormogonia; tapering filaments; and the differentiation of filaments into purely vegetative parts and cells producing gonidia. While this diversified development does not seem to have led to the evolution of the higher plants, it is evident that many of their varied forms are very successful from the standpoint of the struggle for existence, as is evidenced by their great abundance.

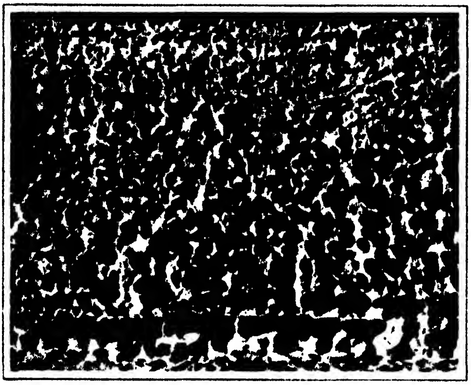


Fig. 442. *Camasia spongiosa*, a Proterozoic fossil believed to have been formed by the action of a blue-green alga. (× ⅔)

After Walcott

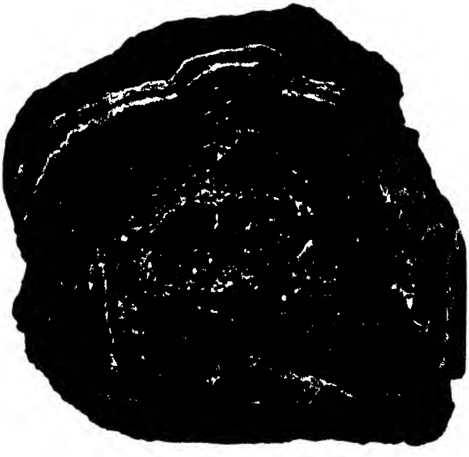


Fig. 443. *Collenia undosa*, a Proterozoic fossil believed to have been formed by the action of a blue-green alga

After Walcott

In view of our lack of information, our ideas as to the relationship of the bacteria, the blue-green algae, and other simple plants can be only speculations. It is reasonable to suppose that the most primitive plants lacked chlorophyll and that the bacteria give us our best idea of a great group of plants which may have been the ancestors of all higher plants. The members of any such great group must have evolved along various lines, some of which may be represented by the bacteria as we know them. Perhaps another line evolved into a group, now extinct, the members of which moved by means of flagella and had chlorophyll diffused in the protoplasm. One branch of this group may have lost its flagella, a process which has occurred more than once in the evolution of the plant kingdom, and developed into the blue-green algae, while another line retained its flagella, developed chloroplasts and true nuclei, and gave rise to the simpler green algae, and through them to all higher plants. We must remember, however, that such ideas, even though they may be fascinating and may seem reasonable to some, are only speculations; and that, as with most speculations, there is bound to be a diversity of opinion.

CHAPTER XIX

FLAGELLATES, THE ANCESTORS OF ALGAE AND HIGHER PLANTS

General characteristics. The flagellates are aquatic organisms which combine plant characteristics with those that we ordinarily associate with animals to such an extent that they seem to be, as it were, at the parting of the ways between the plant and animal kingdoms. Many of them are single-cell individuals (Fig. 444). In numerous other cases individuals are associated in colonies (Figs. 579, 580), which are held together in various ways. In such cases, however, the colony is merely an association of individuals which are not united in an intimate manner like the cells in the tissues of the higher plants. Each individual of the colony is largely in-

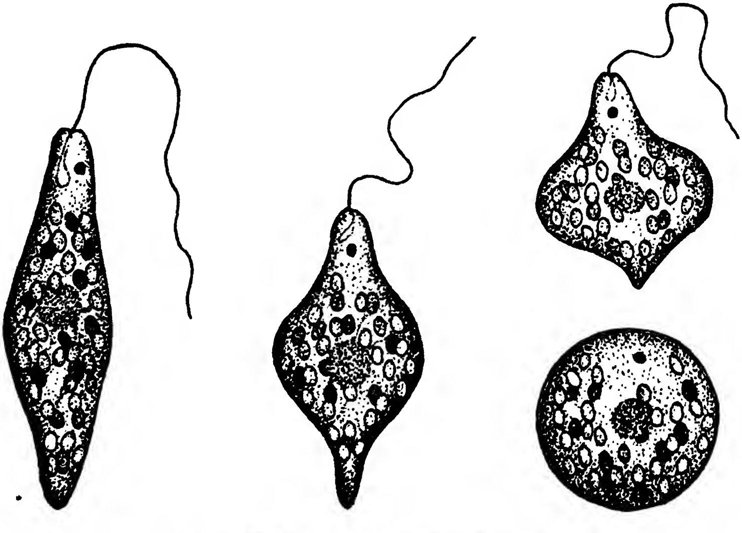


FIG. 444. *Euglena,* showing various forms assumed by a single cell. (× 675)

dependent of the other individuals and has its own nutritional processes. Each individual flagellate when in a motile state has one or two (rarely more) slender hairlike projections called flagella, the movements of which enable the individual to swim in water (Figs. 445–448). Long and rather coarse cilia are called flagella, and the flagellates owe their name to the characteristic presence of flagella.

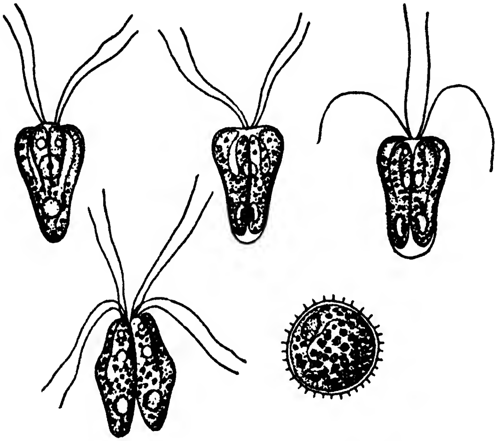


FIG. 445. *Pyramidomonas tetrarhynchus*, a flagellate with four flagella and a four-lobed anterior end

The figure shows a mature individual, three stages in the division of one individual into two, and an encysted individual. (After Dill)

The flagellates are generally said to be distinguished from algae by being naked cells, while algae have cell walls, usually of cellulose; also by lacking sexual reproduction. Algae are believed to be descended from flagellates, and so it is not surprising that there should be no sharp line of separation and that some flagellates should have a mixture of flagellate and algal characteristics. Thus among the flagellates we find a few with sexual reproduction (Fig. 447) and some with cellulose walls. The distinction between flagellates and algae is thus an arbitrary one. Organisms which have cell walls and sexual reproduction are algae, while those which lack them are placed in the flagellates.

It is characteristic of flagellates to become encysted; that is, to lose their flagella and become surrounded by a thick firm covering (Figs. 445–448). While encysted they are resistant to adverse conditions such as drying, and so can persist through unfavorable periods which would be fatal to active individuals. Also, encysted individuals are in a favorable condition to be carried from place to place by the wind, on the feet of birds, and in other ways.

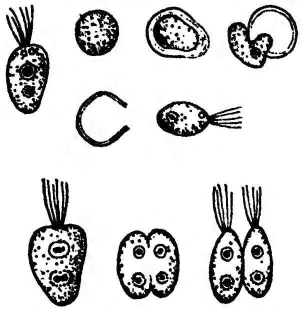


Fig. 446. ***Polyblepharides singularis*, a flagellate with several flagella**

Above, mature individual, a rounded cyst beginning to germinate, flagellate escaping from the cyst, flagellate escaped from the cyst. Below, division of a single individual to form two daughter individuals. (After Dangeard)

Some flagellates have well-developed green, yellow, or brown plastids which enable them to carry on photosynthesis; others are colorless and live by absorbing organic matter from the surrounding water; many can take in and digest solid particles. Some forms contain chlorophyll and manufacture food by photosynthesis when living in the light, but when growing in the dark in nutrient solutions they lose their chlorophyll and absorb organic food from the surrounding medium (Fig. 448). Plastids which are bright green owing to an abundance of chlorophyll are called chloroplasts. Those in which the green color of chlorophyll

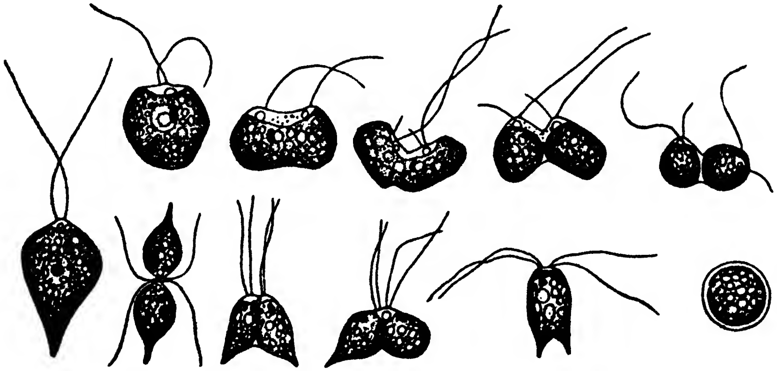


Fig. 447. ***Phyllocardium complanatum***

Left, a mature individual. Note two contractile vacuoles near the base of the flagella. There is a single large chloroplast which fills most of the peripheral part of the cell. In the center is a single nucleus and just above this an eyespot which in the drawing is black. Upper row, stages in division of one individual to form two. Lower row, fusion of two small individuals (gametes) to form a single cell. This flagellate has many features which must have characterized the flagellate ancestors of green plants. (× 900). After Korshikov

is masked by a pigment of another color are known as chromatophores, a more inclusive term which includes all colored plastids. Various types of chromatophores are found in the flagellates. As the photosynthetic pigments of the flagellates occur in definite plastids, the flagellates are more advanced in this respect than are the blue-green algae, where the pigment is diffused throughout the peripheral part of the cell. Flagellates have a single definite nucleus with a nuclear membrane, and in this respect also are more advanced than the blue-green

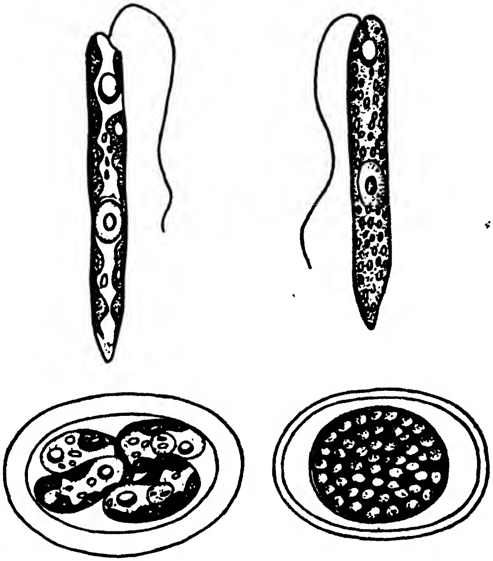


FIG. 448. *Euglena gracilis*

Upper right, green form; upper left, colorless form grown in nutrient solution in the dark; lower right, encysted form; lower left, contents of cyst divided to form four daughter cells. (Redrawn after Zumstein)

EUGLENA, A COMMON FLAGELLATE

General characteristics. *Euglena* (Figs. 444, 448) is a very common and well-known genus of unicellular flagellates which is frequently so abundant in small puddles of standing water as to give the water a greenish color. The cells are naked, but the outer layer of protoplasm (periplast) is somewhat stiff. In some species it is too stiff to permit the organism to change its form, while in others it is soft enough so that the individual may show marked change in shape when not actively swimming. This change in shape may result in a sort of creeping movement. Within the cell are a single nucleus and a number of green plastids, which in most species are disk-shaped (Fig. 444). The green color is due to an abundance of chlorophyll. At the anterior end is a single flagellum. At the base of the flagellum is a large contractile or pulsating vacuole which alternately contracts and expands, and near this is a conspicuous red spot called an eyespot.

In *Euglena* the large contractile vacuole discharges into a canal-like depression in the anterior end of the cell (Fig. 449). Around the large vacuole is a system of smaller ones which empty into it. Contractile vacuoles are characteristic of flagellates and are widespread in the motile cells of primitive algae. The system is usually much less complex than in *Euglena*, and in most cases there is a single vacuole, or two which contract alternately. In many cases they discharge into the surrounding cytoplasm. Most authorities regard contractile vacuoles as organs of excretion, but their exact function is still in question.

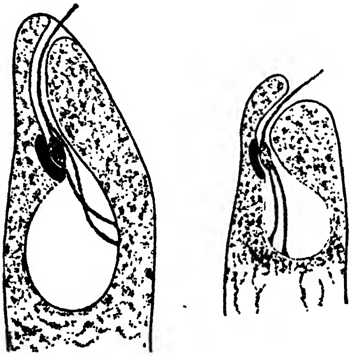


Fig. 449. Anterior end of *Euglena viridis* seen in section

Note attachment of flagellum to interior of contractile vacuole. On the left of the enlargement of the flagellum is the eyespot, which in the drawing is black. (After Wager)

An eyespot is found in many flagellates, and, like the contractile vacuole, is characteristic of many of the more primitive algae. In some of the lower plants it has been shown to consist of two parts, a pigmented cup-shaped structure and a clear lens-shaped portion which fits into the former (Fig. 477). It is generally assumed that the clear part is sensitive to light, while the pigmented portion acts as a shield, and that the eyespot plays a part in causing the organism to orient itself in reference to the direction of the light. However, motile organisms without eyespots are also sensitive to light.

Reproduction. As in typical flagellates, *Euglena* reproduces by the longitudinal division of the motile cells (Fig. 450). Also, the cells may become encysted, in which case an individual comes to rest, rounds up, loses its flagellum, and encases itself in a thick wall. While it is in this condition the protoplasm may divide to produce a number of small individuals which escape from the wall of the cyst and grow to mature size.

Relationship of flagellates. The flagellates are clearly on the border line between animals and plants, and there are reasons for considering them as the group from which both animals and higher plants have been derived.

While at least those forms which contain chlorophyll may surely be regarded as plants, the whole group is considered by many zoologists as belonging to the animal kingdom, and those forms that lack chlorophyll are certainly like animals in their characteristics. A way in which protozoa (one-celled animals) may have been derived from plants is suggested by those forms which contain chlorophyll and at the same time ingest solid food particles, and by those which under certain conditions contain chlorophyll and obtain food by photosynthesis and under other conditions lack chlorophyll and live like animals. The pigmented and some of the colorless flagellates are clearly related, while transition forms connect pigmented flagellates with the simplest single-celled amoeboid animals.

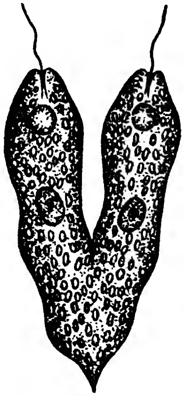


FIG. 450. Division of motile cell of *Euglena*

Redrawn after Stein

Some of the characteristics of the flagellates which at first sight might seem to suggest that they are animals are the very ones that indicate most clearly that they are the ancestors of the higher plants. Movement by means of flagella is found in the simplest plants, the bacteria, and is characteristic of the simpler algae, while similar types of movement are found in reproductive cells of specialized plants even as high in the evolutionary scale as the simplest of the seed plants. Likewise, the presence of an eyespot and contractile vacuoles is characteristic of many of the unicellular plants and of the reproductive cells of many of the simpler of the multicellular ones. A consideration of the flagellates shows very clearly that there is no absolute distinction between plants and animals.

It seems reasonable to suppose that the flagellates were derived from some simpler chlorophyll-bearing plants. The blue-green algae, however, are the only known chlorophyll-bearing plants which are considered as more primitive than the flagellates. In the possession of flagella the flagellates are more like the bacteria than like the blue-green algae. Certainly the way in which the flagellates may be related to these two groups is entirely uncertain.

While the origin of flagellates is obscure, it seems to be established that they have given rise to various groups of algae and probably through them to higher plants.

Classification of flagellates. The flagellates afford a good example of the various ways in which a single group of plants might be classified. Formerly they were regarded as a separate class with various subdivisions. It has been found, however, that most of the groups of flagellates have given rise to algal forms. At present it is more usual to regard a group of flagellates and the algae derived from that group as composing a class of the plant kingdom. Thus, instead of separating the flagellates from the various classes of algae, flagellates and algae are divided into parallel series which, theoretically, in each case might begin with flagellate representatives and end with algae. In some cases the algal and in others the flagellate forms are missing. *Euglena* belongs to a specialized class in which there are no algal members. *Euglena* is convenient for study because some species are common and large forms.

CHAPTER XX

CHLOROPHYTA, THE GREEN ALGAE

INTRODUCTION

General characteristics. The green algae are very common and widely distributed plants. The small and simpler ones are of microscopic size (Fig. 451), but some of them are frequently present in sufficient abundance to render them conspicuous. The primitive plants are generally believed to have been aquatic. While some green algae live in aerial situations (Fig. 504), the great majority live in water and have retained the primitive characteristics which fit them for an aquatic habitat. Larger forms are frequently very abundant and conspicuous in streams and pools (Figs. 491, 492), and can be distinguished from seed plants by their simple organization. Marine green algae are also numerous (Fig. 493). While very few have any direct use, and these are of no great value, the green algæ are very important as a source of food for aquatic animals.

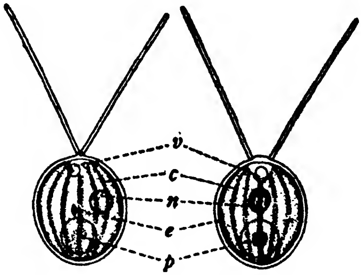


FIG. 451. **Diagram showing two side views of *Chlamydomonas nasuta***

v, contractile vacuole; *c*, chloroplast; *n*, nucleus; *e*, eyespot; *p*, pyrenoid. Note the ridges on the chloroplast. This is a characteristic found in some species of *Chlamydomonas*. In the drawing to the left, two contractile vacuoles are shown, one expanded, the other contracted. In the drawing on the right, one contractile vacuole is hidden. (After Kater)

The green algae form a large and diversified group of plants. They get their name from their characteristic green color. The chlorophyll and associated pigments are found in chloroplasts, and are the same and occur in much the same proportions as in the chloroplasts of the seed plants. It is due to this similarity in pig-

ments that green algae and higher plants have much the same color. This similarity is also one of the reasons for believing that the higher plants are descended from green algae.

Green algae are very varied in form, and it is evident that they have undergone evolution in a number of different directions. They vary in size from single-celled individuals (Fig. 452) to sheets of very considerable size (Fig. 493). In a number of different lines, they show an evolution of the differentiation of sex. In the simplest forms of sexual reproduction the cells (gametes) which fuse (Fig. 452) are similar (isogametes). In a more advanced stage (Fig. 498) the gametes differ in size (heterogametes). Finally, there may be the fertilization of a large non-motile female cell (egg) by a small motile male cell or spermatozoid (Figs. 499, 510).

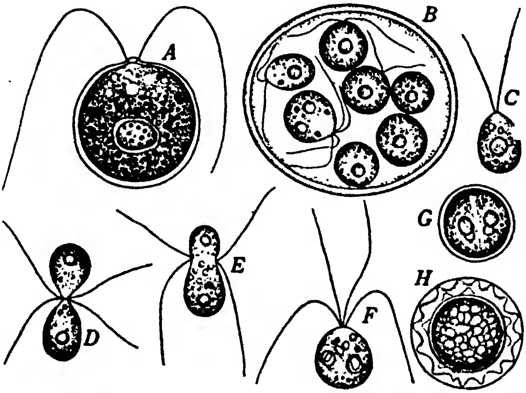


Fig. 452. ***Chlamydomonas pertu***

A, mature individual; note that the cell is rather round and that there are several contractile vacuoles. *B*, gametes formed within the wall of the mother cell; two have fused to form one individual with four flagella. *C*, gamete; note the contractile vacuoles and eyespot. *D*, *E*, *F*, stages in fusion of gametes. *G*, young zygote. *H*, mature zygote. (After Goroschankin)

Despite their diversity, green algae have certain points in common. In addition to having the same pigments as the higher plants, they, like the higher plants, store food in the form of starch and have cellulose in their cell walls. The chloroplasts of most of the green algae contain one or more bodies known as pyrenoids. A pyrenoid usually consists of a central protein portion which is surrounded by minute starch grains. The pyrenoids are generally believed to be connected with the formation of starch; but starch may be formed by species which lack pyrenoids, or away from pyrenoids when they are present.

The green algae are a very interesting group because of the great diversity of forms, because many of them are common and widely distributed, and because the higher plants are generally believed to have evolved from some form of green alga.

ORDER VOLVOCALES, THE MOTILE GREEN ALGAE

Chlamydomonas, a Primitive Green Alga

Cell structure. The genus *Chlamydomonas* is an interesting unicellular form which is clearly intermediate between the flagellates and many of the higher green algae. The cells of *Chlamydomonas* are spherical, oval, or somewhat cylindrical (Figs. 451–455). They are surrounded by cell walls, and each individual has two flagella at its anterior end. The protoplasm at the anterior end is clear and contains contractile or pulsating vacuoles, which are usually two in number and contract alternately. Most species of *Chlamydomonas* have a red eyespot, which is usually at or near the anterior end. The cell contains a chloroplast which, typically, is cup-shaped and contains a pyrenoid. *Chlamydomonas* has a single

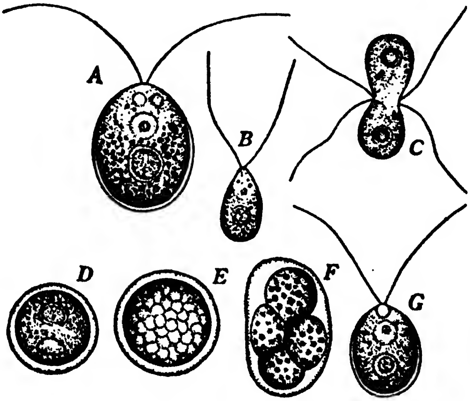


FIG. 453. *Chlamydomonas reinhardi*

A, mature individual; as in most species of *Chlamydomonas*, there are two contractile vacuoles; note nucleus below the vacuoles, eyespot to the right of the nucleus, and the conspicuous pyrenoid below the nucleus. *B*, gamete. *C*, gametes fusing. *D*, young zygote. *E*, mature zygote. *F*, contents of zygote divided to form zoospores. *G*, a zoospore. (After Goroschankin) nucleus. The nucleus, like those of other green algae, is highly developed, is sharply limited by a nuclear membrane, and divides by mitosis (Fig. 456). In all these respects, other than the presence of a cell wall, *Chlamydomonas* is very similar to the flagellates from which the green algae are derived (Fig. 447). Although *Chlamydomonas* is a small organism, the different species vary from each other considerably in various details (Figs. 451–455).

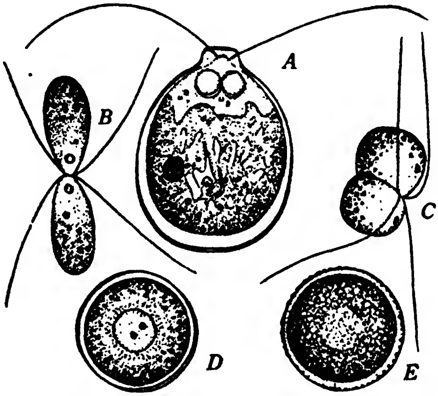


Fig. 454. *Chlamydomonas reticulata*

A, mature individual; note that the chloroplast is reticulate and that the contractile vacuoles are prominent; the eyespot is seen to the left of the cell. *B*, *C*, gametes fusing. *D*, young zygote. *E*, mature zygote. (After Goroschankin)

Asexual reproduction. *Chlamydomonas* reproduces asexually by the formation of zoospores, a method which is characteristic of many green algae. Zoospores are motile spores. In the formation of zoospores in *Chlamydomonas*, the contents of the cell divide rapidly into two, four, or eight parts (Fig. 457). Each of these acquires the structure of a mature individual, and all are set free from the mother cell by the conversion of the wall of the latter into mucilaginous material. They then grow and become mature motile individuals. The zoospores are simply small individuals.

The method by which one cell becomes divided into two is very different from that seen in the vegetative divisions of higher plants and filamentous algae. In the latter the cell walls of the mother cell remain as walls of the daughter cells, while the mother cell is divided into two by the formation of a cross wall. In *Chlamydomonas* the cell wall does not take part in the division, this being confined to the protoplast (Figs. 457, 458). The newly formed protoplasts surround themselves with new cell walls, while the cell wall of the mother cell goes to pieces and disappears. The division of the protoplast is, therefore, similar to the division of a flagellate.

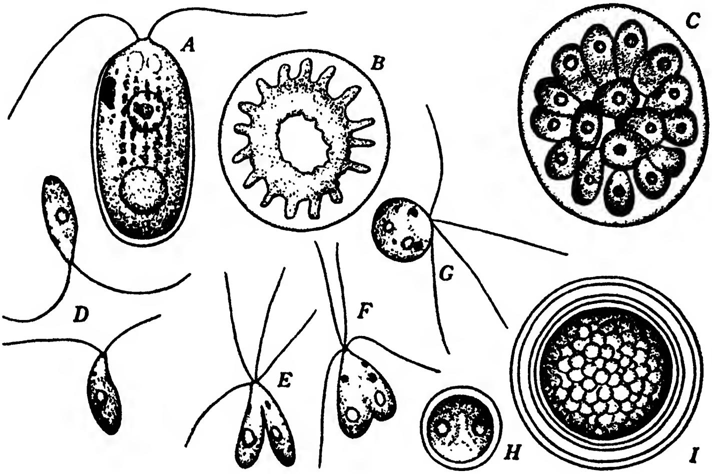


FIG. 455. *Chlamydomonas steinii*

A, mature individual; note ridges on the chloroplast; above are two prominent contractile vacuoles; below these is the nucleus; in the lower part of the cell is the pyrenoid; in the upper portion, to the left, is the eyespot. *B*, cross section of an individual, showing shape of chloroplast. *C*, gametes formed within the wall of the mother cell. *D*, gametes. *E*, *F*, *G*, stages in fusion of gametes. *H*, young zygote. *I*, mature zygote. Compare Figs. 451–454, and note differences between different species. (After Goroschankin)

Chlamydomonas has what is known as a palmella stage, during which it loses its flagella and may divide to form numerous individuals. The cells, instead of escaping from the gelatinized mother-cell wall, remain within it and are held together in a gelatinous matrix (Fig. 458), formed by the gelatinization of the cell walls of successive generations. When conditions again become favorable to the motile stage, the cells acquire flagella and swim out of the jelly.

Sexual reproduction. Sexual reproduction takes place by means of gametes, which are formed in the same way as zoospores and have the same general structure, but are smaller and more numerous (Figs. 452–455, 459). Two of these fuse together to form a single cell known as a zygote. This surrounds itself with a thick wall and becomes a zygospore, which undergoes a period of rest.

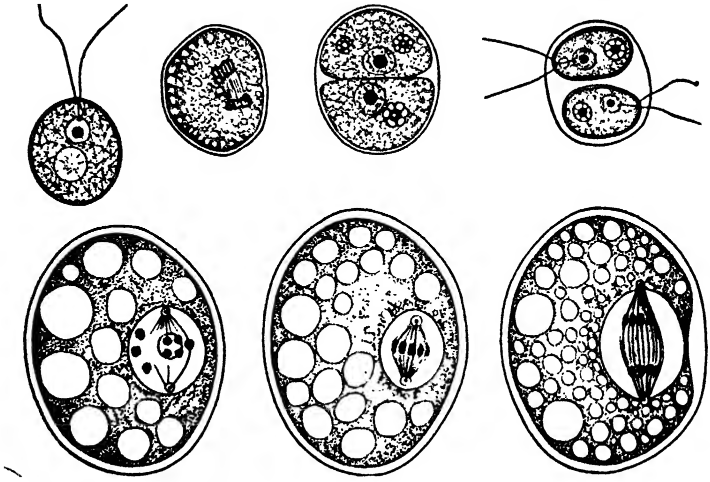


FIG. 456. *Chlamydomonas nasuta* stained to show structure

Upper left, mature individual. Note nucleus above and pyrenoid below. Next three figures represent division of the protoplast of one individual to form two daughter individuals. Lower line, prophase, metaphase, and anaphase of mitosis. (After Kater)

A zygospore is a spore formed as a result of the fusion of two gametes. Zygospores are very resistant to adverse conditions, and they enable *Chlamydomonas* to survive through periods when the environment is unfavorable. When conditions are favorable, the contents of zygospores are transformed into zoospores, which enlarge and become mature motile individuals. In most cases (Fig. 459) the gametes of *Chlamydomonas* are all alike (isogametes); in one case (Fig. 460) they differ in size (heterogametes).

The similarity of the gametes and zoospores of *Chlamydomonas* indicates that in such cases gametes have been derived from zoo-

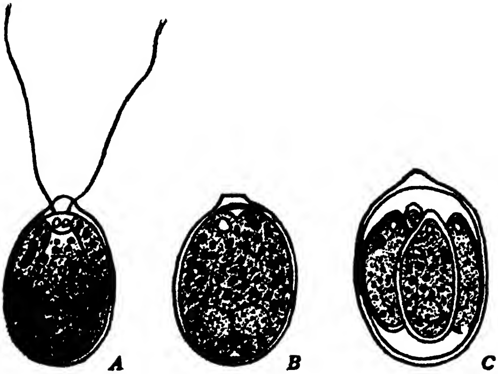


Fig. 457. Division of *Chlamydomonas angulosa* into daughter cells

Note that in *C* the wall of the mother individual is intact and that the daughter individuals have surrounded themselves with new walls. (Redrawn after Dill)

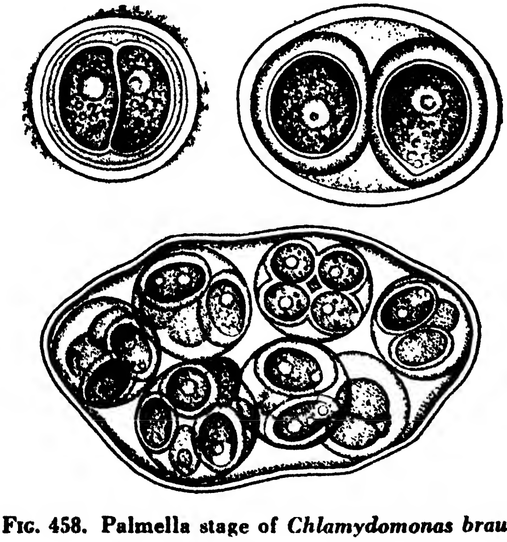


Fig. 458. Palmella stage of *Chlamydomonas braunii*

After Goroschankin

spores and that sexuality had its origin in the transformation of non-sexual zoospores into sexual gametes.

Unicellular algae related to *Chlamydomonas*. There are a number of unicellular green algae more or less closely related to *Chlamydomonas*. Only two which represent different types and belong to different families or subfamilies will be mentioned here. *Carteria* differs from *Chlamydomonas* chiefly in that it has four instead of two flagella (Fig. 461). In *Sphaerella* (*Haematococcus*) the cell wall consists of a firm outer layer and a thick gelatinous inner layer which is transversed by thin strands from the protoplast (Fig. 462). This form has two flagella and a single chloroplast with several pyrenoids. A red pigment, haematochrome, may be so abundant in either motile individuals or resting cells as to give them a red color. *Sphaerella* reproduces asexually by the division of the protoplast of a motile individual to form zoospores which, like those of *Chlamydomonas*, are

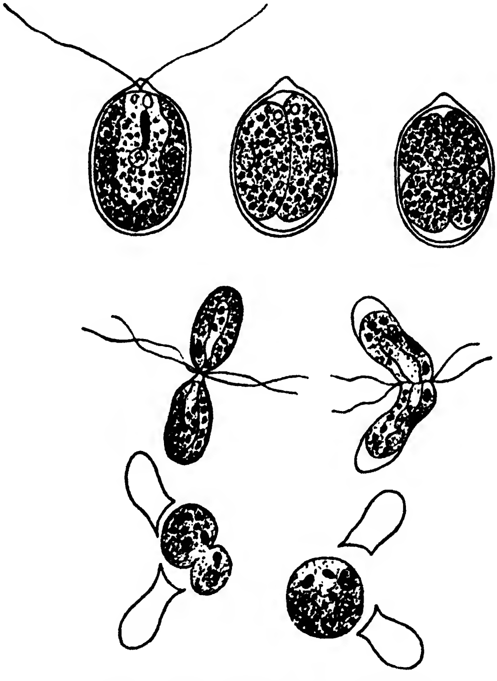


FIG. 459. *Chlamydomonas longistigma*

Above, division into daughter cells; lower figures show the conjugation of gametes. (Redrawn after Dill) small individuals (Fig. 462). It is very characteristic of *Sphaerella* to lose its flagella and to form non-motile cells the contents of which may divide to form other non-motile cells (Fig. 462) or palmella colonies. Also, the contents of non-motile cells may divide up to form either zoospores or isogametes.

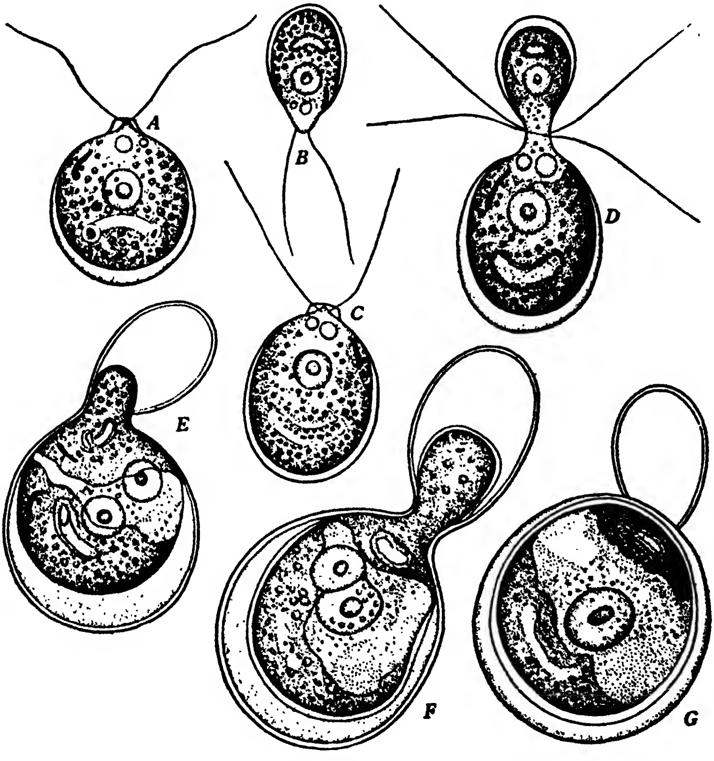


FIG. 460. *Chlamydomonas braunii*

A, mature individual; *B*, small gamete; *C*, large gamete; *D*, *E*, *F*, stages in fusion; *G*, zygote. (After Goroschankin)

Relationship. *Chlamydomonas* and closely related forms seem clearly to be descended from a family of green flagellates (the *Polyblepharidaceae*). This family of flagellates (Figs. 445–447) is the most primitive family of the green algal series, and *Chlamydomonas* is so similar to some of its members that if *Chlamydomonas* did not have a cell wall it would be included in it. Sexual reproduction has not been reported in the more primitive members of the family, but in an advanced one there is a fusion of isogametes (Fig. 447) similar to that in *Chlamydomonas.*

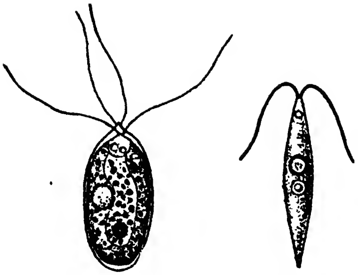


Fig. 461. Two relatives of *Chlamydomonas*

Left, *Carteria,* which has four flagella; right, *Chlorogonium,* which differs from *Chlamydomonas* largely in being long and slender. (After Dill and Franze)

The members of the *Polyblepharidaceae* resemble *Chlamydomonas* in possessing a single large chloroplast with pigmentation similar to that of other green algae. They also resemble *Chlamydomonas* in manufacturing starch, and in most cases there is a pyrenoid within the chloroplast. As in *Chlamydomonas,* the individuals have a single eyespot. The number of flagella varies from two to four and eight with the different genera. In some cases there are two contractile vacuoles, as is usual in *Chlamydomonas.* As in *Chlamydomonas,* there is a highly developed nucleus which has a nuclear membrane and which divides mitotically.

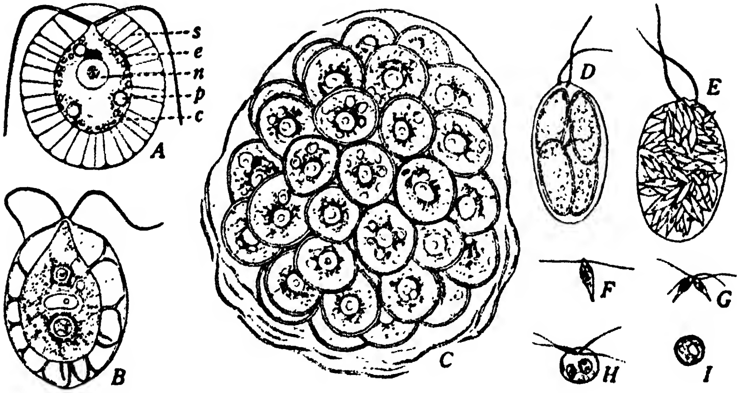


Fig. 462. *Sphaerella*

A, Sphaerella pluvialis: *s,* strand of protoplasm reaching from protoplast to cell wall; *e,* eyespot; *n,* nucleus; *p,* pyrenoid; *c,* chloroplast. *B, Sphaerella droebakensis. C,* palmella stage of *Sphaerella pluvialis. D,* individual of *Sphaerella droebakensis*; the contents have divided to form four zoospores. *E,* many gametes within the mother cell. *F,* gamete. *G, H,* fusion of gametes. *I,* zygote. (After Reichenow and Wollenweber)

In the green algae there are, as previously mentioned, quite a number of different lines of evolution, and several of these appear to have started from *Chlamydomonas* or similar forms.

From the considerations given above it appears that *Chlamydomonas* and closely related unicellular forms are very primitive green algae. A consideration of *Chlamydomonas* and its near relatives among the unicellular green algae and green flagellates should therefore indicate those features which are characteristic of primitive green algae. We may conclude that among the structures which characterize the most primitive green algae are flagella, contractile vacuoles, an eyespot, a single cup-shaped chloroplast, and, in those which are algae rather than flagellates, a cell wall containing cellulose. The primitive green algae are unicellular and motile. The division of the protoplast is not due to the formation of cross walls but to the activity of the protoplast itself; the old cell wall disintegrates, while the new protoplasts form new cell walls around themselves. New individuals are like the parent ones except for size. The simple green algae reproduce sexually as well as asexually; sexual reproduction is due to the fusion of isogametes.

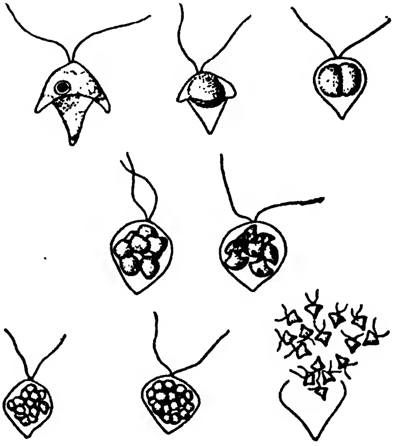


FIG. 463. ***Brachiomonas submarina*, a relative of *Chlamydomonas***

First two lines, a mature individual and division of protoplast to form zoospores; last line, formation of gametes. (After Teodoresco)

Volvox, a Colonial Green Alga

General characteristics. The genus *Volvox* contains a number of species of colonial algae (Figs. 464–469) which are very common in fresh-water ponds and sometimes occur in great abundance in lakes. They are more or less the size of a pinhead, and are among

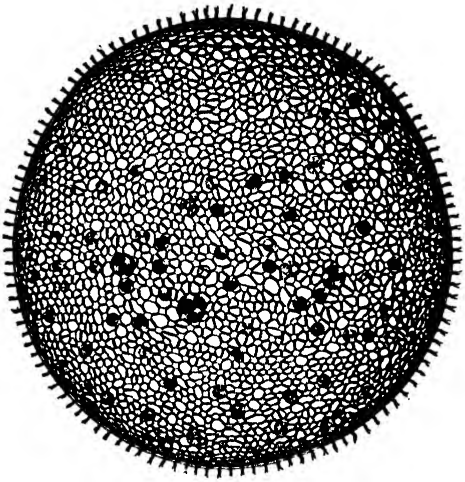


Fig. 464. *Volvox merrillii*

A colony within which are many young eggs (the smaller round homogeneous bodies) and a few groups of spermatozoids. The latter are larger than the young eggs in the drawing and can be seen to be composed of a number of individual spermatozoids. Note that there are prominent protoplasmic strands connecting the individuals of the colony. (× 100)

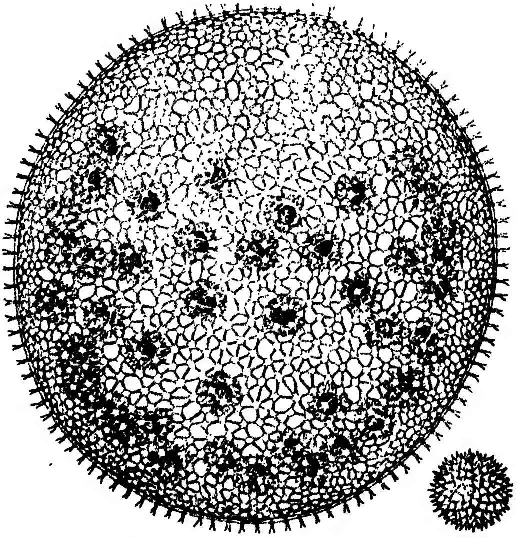


Fig. 465. ***Volvox merrillii*, a colony within which are many oospores. (× 100)**

Lower right, a single oospore showing spiny cell wall

the most beautiful and fascinating objects in the plant kingdom. A colony may contain as few as five hundred cells, but usually they are several thousand. The cells are arranged in a single layer at the periphery of the colony and are surrounded by a gelatinous matrix (Figs. 465, 467). The center of the colony may contain thinner gelatinous material or water. In some species the individual cells are connected with each other by prominent protoplasmic strands (Figs. 464, 465), in others by fine strands, while in still other species connecting strands have not been demonstrated (Figs. 466, 468). However, there is indirect evidence that protoplasmic connections between cells, perhaps very fine ones in some cases, are of general occurrence in *Volvox* and related genera. The individual cells are much like those of *Chlamydomonas*. They have two flagella, contractile vacuoles, an eyespot, and a single chloroplast which is often cup-shaped and usually has a single pyrenoid. *Volvox*

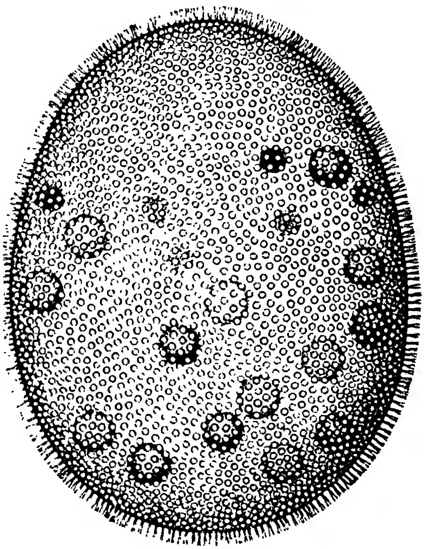


Fig. 466. ***Volvox*** **(*Merrillosphaera*) africana, a bisexual colony**

Note that no connecting strands are visible between the cells of the colony. The large cells within the colony are oospores. The six smaller bodies are groups of spermatozoids. (× 165) may, therefore, be thought of as a colony of *Chlamydomonas*-like individuals.

A *Volvox* colony may swim about rather rapidly by the movements of the flagella of individual cells. The cells are so arranged

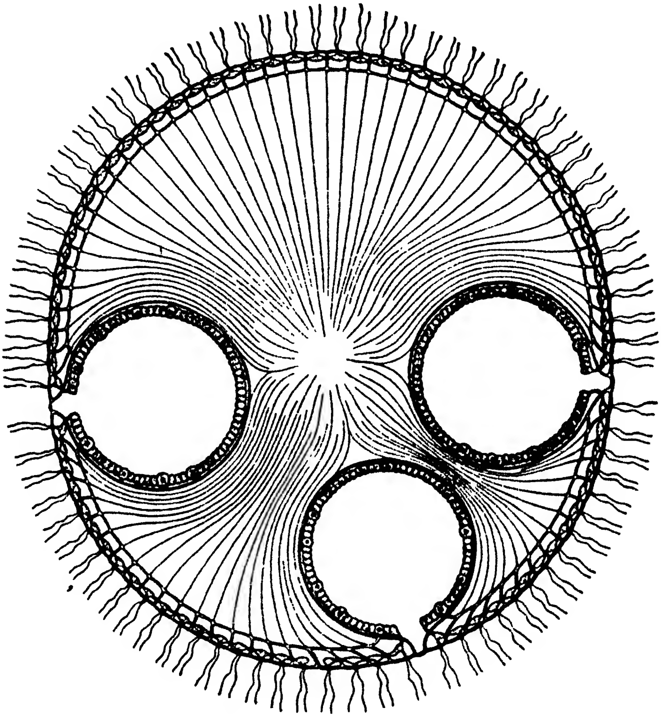


Fig. 467. ***Volvox globator.*** **A somewhat diagrammatic section through a colony in which three daughter colonies are developing**

Note that the reproductive cells are already differentiated in the daughter colonies. (After Janet)

that the smaller anterior end points outward. The flagella are attached to this end and project out of the gelatinous matrix (Figs. 467, 469). Nearly all the cells of a *Volvox* colony are vegetative cells and remain so throughout the life of the colony. Depending on the species and circumstances, the reproductive cells produced by a colony may be either sexual (Fig. 465) or asexual (Fig. 467) or both sexual and asexual.

Asexual reproduction of *Volvox*. In a *Volvox* colony which is destined to reproduce vegetatively, a few cells in the posterior end enlarge, move toward the center of the colony, and lose their flagella. Each cell then divides up to form a new colony, which develops to a considerable size while within the parent colony (Fig. 467). Finally the parent colony disintegrates and the daughter colonies are set free. Often granddaughter colonies appear within the daughter colonies while the latter are still within the parent colony (Fig. 468).

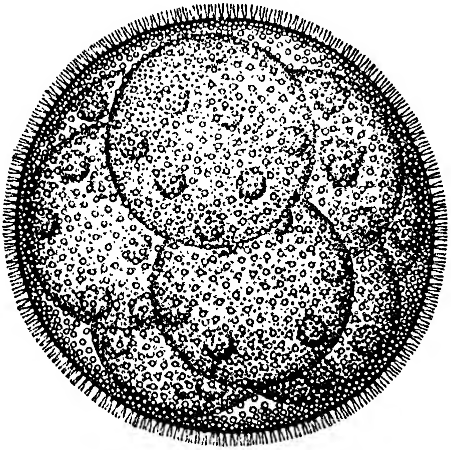


FIG. 468. *Volvox* (*Merrillosphaera*) *carteri*

Note the large asexual daughter colonies within the mother colony and the granddaughter colonies within the daughter colonies. Note also that no protoplasmic connections are visible

Sexual reproduction of *Volvox*. In sexual reproduction either a few or a considerable number of cells in the posterior part of the colony become differentiated. Male and female cells may be found either in the same (Figs. 464, 466, 469) or in different colonies (Fig. 465). The male cells are biflagellate spermatozoids and are produced in large numbers by the division of a single cell (Fig. 469). The female cells are eggs (Fig. 469). Each egg is formed by the enlargement of a single cell which loses its flagella and becomes rounded and very much larger than a vegetative cell. The spermatozoids swim actively in the water and reach the eggs. A single spermatozoid enters an egg, and its nucleus fuses with the egg nucleus, thus effecting fertilization. This fertilized egg, or zygote, surrounds itself with a heavy cell wall and becomes an *oospore,* which is a spore formed from a fertilized egg. The cell wall of the oospore may be either smooth (Fig. 466) or spiny (Fig. 465). The oospore is a resting spore and can resist adverse conditions such as the drying up of a pond in which the *Volvox* is growing, and then germinate when conditions again become favorable. During the germination of the oospore, the thick outer wall splits and the developing contents, surrounded by the inner layer of the wall, escape (Fig. 470). The protoplast divides up to form a colony in much the same manner as when an asexual reproductive cell produces a colony (Fig. 470).

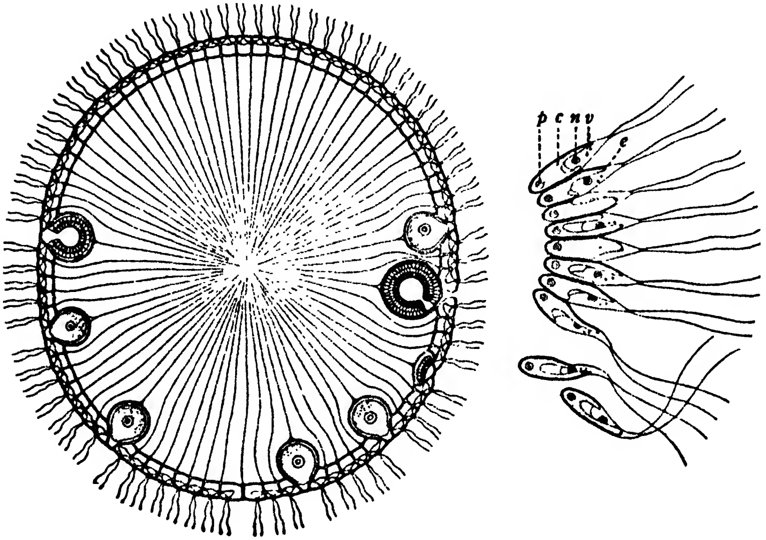


FIG. 469. Left, a somewhat diagrammatic section of a sexual colony of *Volvox globator.* Right, group of spermatozoids of *Volvox aureus*

The large single cells which project inward are the eggs, while the groups of cells similarly projecting inward are spermatozoids in various stages of development. *p,* pyrenoid; *c,* chloroplast; *n,* nucleus; *v,* contractile vacuoles; *e,* eyespot. (After Janet)

In one species (*Volvox rousseletii*) the protoplast of the oospore becomes converted into a zoospore (Fig. 471) which in structure is very much like an individual of *Chlamydomonas*. This emphasizes the relationship of *Volvox* to *Chlamydomonas*. This zoospore divides up to a form a colony. A very curious feature in the development of colonies, whether formed from asexual cells within a mother colony or from the protoplast of a zygote, is that at a rather late stage the colony turns completely inside out. The flagella are produced before this inversion and project inward. Inversion places them at the periphery of the colony. Sperm colonies also undergo inversion.

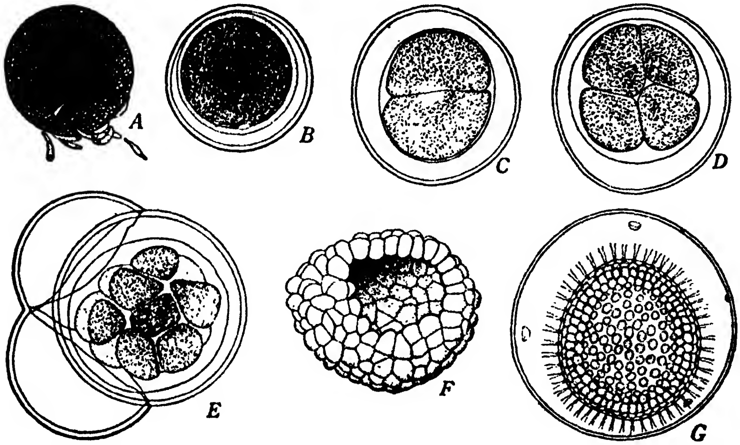


Fig. 470. Development of oospore in young colony of *Volvox minor*

A, an egg near which are many spermatozoids; *B*, oospore; *C*, oospore with contents divided to form two cells; *D*, to form four cells; *E*, the multicellular embryo surrounded by the inner layer of the cell wall escaping from the outer layer; *F*, an older stage in development shown without the cell wall (note that the cells are arranged in the form of a hollow sphere); *G*, young individual within the inner wall of the oospore. (× 300). After Kirchner

Relationship of *Volvox*. The genus *Volvox* is the culmination of one line of evolution which may be traced back to *Chlamydomonas* as a similar simple alga. *Chlamydomonas* and *Volvox*, with the colonial forms of varying degrees of complexity which connect them, compose one of the most beautiful of all known evolutionary series. The simplest of the colonial forms consists of four cells, and is just the type of colony that would result if four zoospores

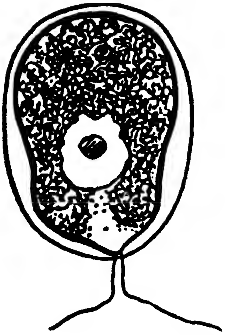


Fig. 471. A zoospore of *Volvox rousseletii*

This zoospore is formed within the oospore and after escaping divides up to form a colony. (× 750). After Pocock

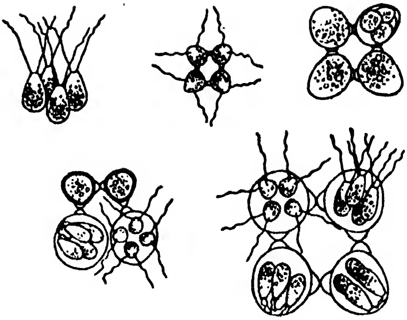


Fig. 472. *Gonium sociale*, a colony of four *Chlamydomonas*-like cells

Side and top view of a colony and stages in division of cells of colony to form daughter colonies. (× 300). After West and West

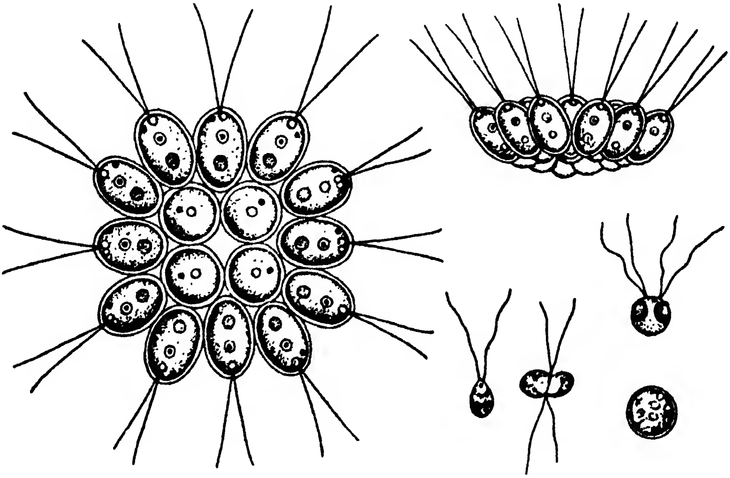


Fig. 473. *Gonium pectorale*

Top and side view of a colony, gamete, and fusion of gametes to form zygote. (After Stein and Schussnig) produced by the division of a *Chlamydomonas* cell, instead of separating, held together until they reached maturity (Fig. 472). Between this small colony and the large ones of *Volvox* there are various intermediate forms (Fig. 565, left). Along with the increasing number of cells in the colony, other specializations have occurred. In the simple colonies all cells are reproductive (Figs. 472, 475). In a somewhat more advanced one, a few cells remain small and vegetative while the majority are larger and are reproductive (Fig. 479). Then there is a form in which about half are small and vegetative (Fig. 480). Finally, in *Volvox* only a few are reproductive (Fig. 465). In the simpler colonies sexual reproduction is isogamous as in *Chlamydomonas* (Fig. 473); in an intermediate form the fusing cells are similar except that the female are much larger than the male (Fig. 476); in *Volvox* we have highly differentiated eggs and spermatozoids. Connecting forms between *Chlamydomonas* and *Volvox* are described below in more detail.

THE MOTILE COLONIAL GREEN ALGAE

The order *Volvocales* includes the flagellates of the family *Polyblepharidaceae* as well as *Chlamydomonas* and *Volvox* and intermediate and related forms.

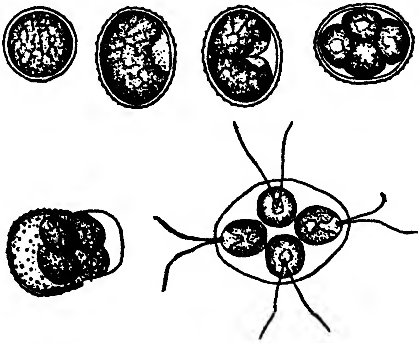


Fig. 474. *Gonium pectorale*

A mature zygote and germination of zygote to form small colony. (× 400). After Schreiber

Gonium. The simplest colonial forms intermediate between *Chlamydomonas* and *Volvox* are in the genus *Gonium*. *Gonium sociale* is a colony of four *Chlamydomonas*-like cells embedded in a common gelatinous matrix. All of the cells are alike, and each can reproduce a colony (Fig. 472).

Another species of *Gonium*, *Gonium pectorale*, is slightly more complex, as the colony consists of a plate of sixteen cells (Fig. 473). Otherwise it is very similar to *Gonium sociale*. Each cell of the colony may divide and produce a new colony. Sexual reproduction is by the fusion of similar gametes (isogametes), as in most species of *Chlamydomonas*. The gametes are formed by the division of one cell of a colony to form sixteen gametes. Two gametes from different colonies fuse to form a single cell or zygospore, which becomes surrounded by a membrane. On germination the contents of the zygospore divide to form four zoospores, which may be united and thus form a small colony (Fig. 474).

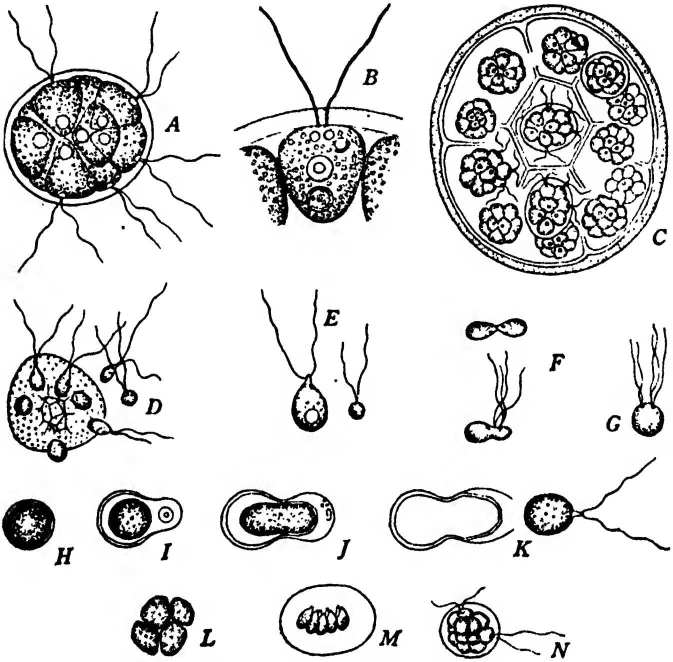


FIG. 475. *Pandorina morum*

A, mature colony; *B*, a single individual (note two contractile vacuoles above, eyespot to the right, nucleus in the center, and pyrenoid near posterior end); *C*, cells of mother colony forming daughter colonies; *D*, gametes escaping from a sexual colony; *E*, large and small gametes; *F*, *G*, fusion of gamete; *H*, zygote; *I*, *J*, *K*, germination of zygote to produce zoospore; *L*, *M*, *N*, division of zoospore to form colony. (× 350). After Pringsheim

Pandorina. This genus shows what may be regarded as a further advance in that the colony has a spherical form (Fig. 475). As in *Gonium*, any cell of the colony may divide to form a new colony. Sexual reproduction results from the fusion of motile gametes produced by the division of a cell of a colony to form sixteen gametes, and is similar to that of *Gonium* except that usually a small active (male) gamete fuses with a larger more sluggish (female) gamete (Fig. 475). This fusion of unequal gametes has been regarded as indicating a very primitive stage in the differentiation of sex.

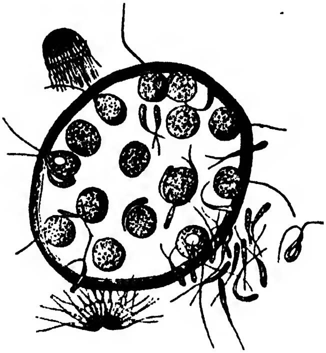


FIG. 476. ***Eudorina elegans***

A female colony with large gametes around which are two bundles of spermatozoids and numerous free spermatozoids some of which are in contact with the large female gametes. (After Goebel)

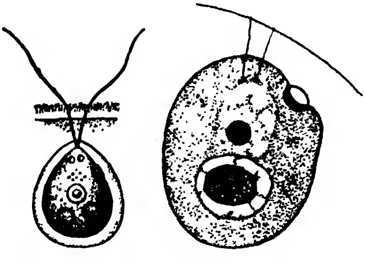


FIG. 477. ***Eudorina elegans***

Left, a single cell (× 325). Note two contractile vacuoles, prominent eyespot, nucleus in the center of the cell, and below two pyrenoids. Right, section of a cell showing lens-shaped clear area in the hollow of the cup-shaped pigmented area of the eyespot. Note section of large pyrenoid in lower part of cell. (After Franze and Mast)

Eudorina. The colony of *Eudorina* consists of usually thirty-two *Chlamydomonas*-like cells loosely arranged near the periphery of a gelatinous matrix (Figs. 476, 477). As in the genera previously described, each cell of a vegetative colony may form a new colony. However, in sexual reproduction there is a distinct differentiation of sexes, which are usually found in separate colonies. Some colonies develop as female. These are similar to vegetative colonies except that the cells enlarge slightly and each functions as an egg (Fig. 476). In male colonies each cell divides to form sixty-four pear-shaped, biflagellate spermatozoids. A spermatozoid fuses with an egg to form an oospore, which, on germination (Fig. 478), produces a new colony.

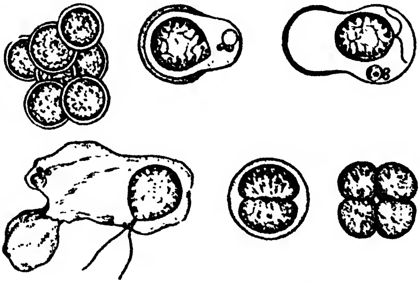


FIG. 478. ***Eudorina elegans***

Zygotes, three stages in germination of zygote to produce zoospore, and two stages in division of zoospore to form colony. (After Schreiber)

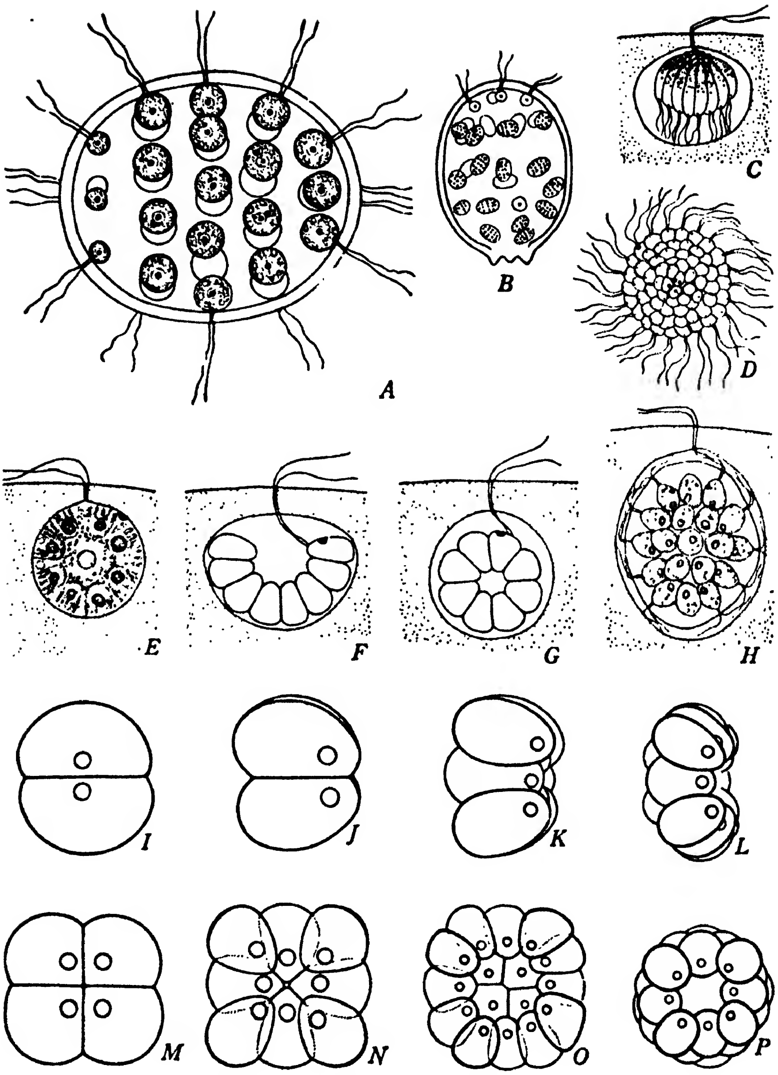


FIG. 479. *Pleodorina illinoiensis*

A, mature colony (× 250); the four small cells to the left are vegetative while all the remainder are reproductive. *B*, the four small anterior cells remain vegetative while the other and larger cells are producing daughter colonies. *C*, *D*, two views of group of sperm cells. *E*–*H*, division of mother cell, while within mother colony, to form a daughter colony. *I*–*L*, side view of division of cell to form daughter colony. *M*–*P*, divisions to form daughter colony, as seen from above. (After Kofoid and Merton)

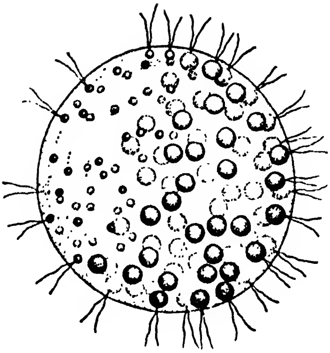


Fig. 480. ***Pleodorina californica***
Note small vegetative cells to the left and larger reproductive cells to the right. (× 150)

Pleodorina. In all the preceding forms any cell of a colony may become reproductive, and so there is no differentiation of vegetative and reproductive cells. Such a differentiation is seen in *Pleodorina. Pleodorina illinoiensis* usually has thirty-two cells as does *Eudorina.* Also, both asexual and sexual reproduction are similar in the two cases. However, in *Pleodorina illinoiensis* four cells in the front or anterior end of the colony are small and remain vegetative, while the others are larger and any of them may reproduce the colony (Fig. 479). The fact that it is the cells in the anterior end which are vegetative would seem to be significant. The differentiation of purely vegetative cells is further advanced in *Pleodorina californica.* Here there are about sixty-four or one hundred and twenty-eight cells, about half of which may be reproductive, while the remainder, located in the anterior end of the colony, are small vegetative cells (Fig. 480).

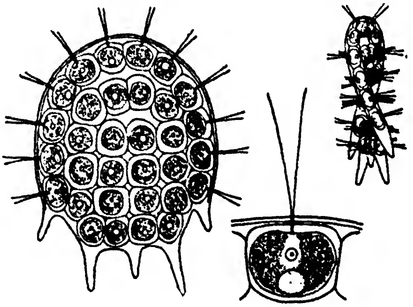


Fig. 481. ***Platydorina*, a flattened colonial form belonging to the *Volvocaceae*.** (× 200)

Left, face view; center, a single cell (note two contractile vacuoles and eyespot at the anterior end, the nucleus in the center, a single large chloroplast around the nucleus, and a large pyrenoid in the chloroplast at posterior end); right, side view of a colony. (After Kofoid)

Volvox. The higher members of the series are placed in the genus *Volvox*, where the cells in a colony are usually very numerous, often as many as twenty-five thousand. Sexual differentiation, which is suggested by the fusion of small and large gametes in *Pandorina* and is very evident in the small spermatozoids and large female gametes of *Eudorina*, reaches its culmination in the spermatozoids and eggs of *Volvox.* The differentiation of vegetative and reproductive cells, which is evident in the four vegetative cells of *Pleodorina illinoiensis* and more pronounced in *Pleodorina californica*, also

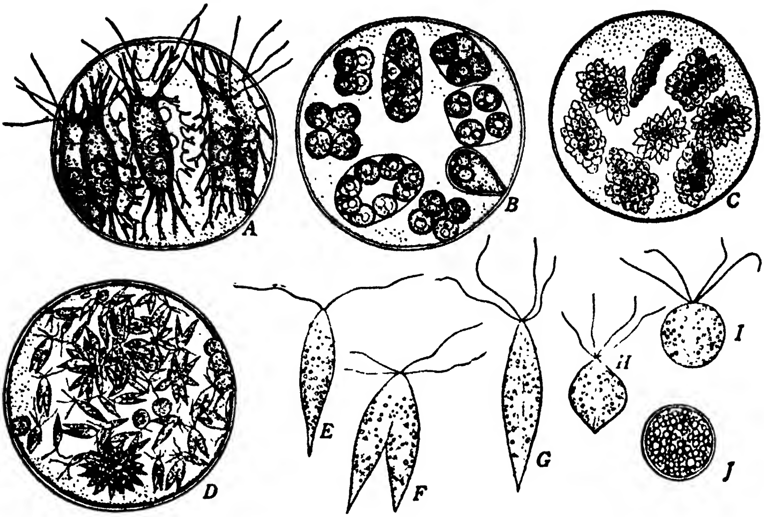


Fig. 482. *Stephanosphaera pluvialis*

A, mature colony; *B*, individuals of a colony giving rise to daughter colonies; *C*, formation of gametes; *D*, later stage with some of the gametes fusing; *E–J*, gamete and fusion of gametes to form zygospore

reaches its culmination in *Volvox*, where thousands of cells may be vegetative and only a comparatively small number are reproductive.

Other colonial *Volvocales*. Included in the *Volvocales* are a number of colonial algae other than those on a more or less direct line from *Chlamydomonas* to *Volvox*. *Platydorina* is a flattened horseshoe-shaped colony of sixteen or thirty-two *Chlamydomonas*-like cells (Fig. 481). All cells are similar and each can produce a new colony. *Platydorina* is believed to be derived from *Eudorina*, which, under certain conditions, can be made to assume a form much like *Platydorina*. *Platydorina* thus appears to be an offshoot from the main line of evolution which has culminated in *Volvox*.

Stephanosphaera is a colony of usually eight cells which are arranged in an equatorial circle within a tough spherical or ellipsoidal covering (Fig. 482). Each protoplast

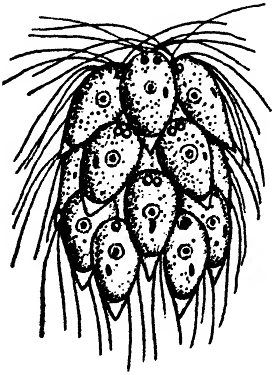


Fig. 483. *Spondylomorum*, a colony of sixteen cells

After Stein

has two flagella which project beyond the covering of the colony. Also each protoplast has protoplasmic processes, like those of *Sphaerella*, which reach to the tough covering of the colony just as those of *Sphaerella* reach to the tough cell wall. *Stephanosphaera* thus appears to be related to *Sphaerella* in much the same way as *Gonium* or *Pandorina* is to *Chlamydomonas*. All the protoplasts of a colony of *Stephanosphaera* are similar, and each can give rise to a daughter colony. Sexual reproduction is by the fusion of two biflagellate isogametes. These are formed in large numbers by the division of the individual protoplasts.

The colony of *Spondylomorum* contains eight or sixteen cells. These are arranged in tiers of four cells, the cells of one tier alternating with those of the next (Fig. 483). Each cell has four flagella. This suggests that *Spondylomorum* may be related to the unicellular *Carteria*, which has four flagella and differs from *Chlamydomonas* only in this respect. There is also a colonial genus similar to *Spondylomorum* except that the cells have only two flagella and are thus similar to the cells of *Chlamydomonas*.

ORDER *TETRASPORALES*, THE PALMELLOID ALGAE

General characteristics. We have seen that motility is characteristic of primitive green algae. The evolution of motile colonies has led to a fairly high degree of differentiation in *Volvox*, but does not seem to have resulted in plants of any considerable size. In contrast to the *Volvocales*, the higher plants are non-motile and are characterized by a great development of vegetative divisions which usually result in a considerable amount of vegetative tissue. A step in this direction is seen in the *Tetrasporales*. In the *Volvocales* the motile condition is dominant and the non-motile is transitory. In the *Tetrasporales* the reverse is true, as in them the non-motile phase is dominant and the motile is transitory. Most of the *Tetrasporales* are colonial forms in which the non-motile cells are held together in a gelatinous matrix formed by the gelatinization of the cell walls of successive generations (Fig. 484).

The ordinary vegetative stage of the *Tetrasporales* is therefore similar to the palmella stage of *Chlamydomonas* (Fig. 458). In them the palmella stage of *Chlamydomonas* has become dominant, while the motile stage is transitory, the reverse of what we have seen in *Chlamydomonas*.

***Palmella*.** The genus *Palmella* is very much like the palmella stage of *Chlamydomonas* (Fig. 458), and consists of a small amorphous colony of spherical or ellipsoidal cells without flagella, held together in a gelatinous matrix. An ordinary vegetative cell can acquire two flagella and swim out of the colony as in *Chlamydomonas*. After moving about for a time, it settles down and by repeated vegetative division forms a new colony. *Palmella* reproduces asexually by the division of the protoplast of a vegetative cell to form zoospores, sexually by the fusion of biflagellate isogametes formed in considerable numbers by the division of the protoplast of a vegetative cell.

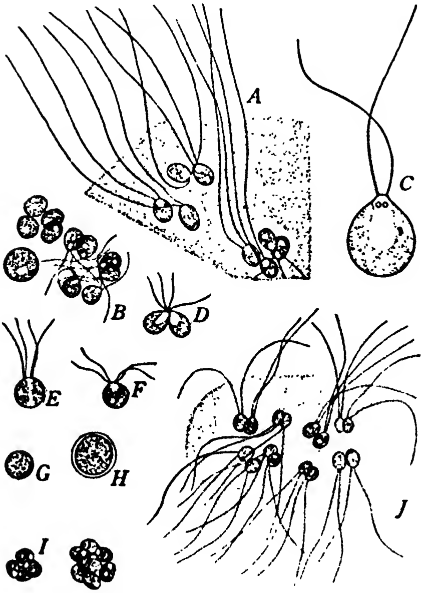


Fig. 484. *Tetraspora*

A, portion of a colony showing vegetative cells with pseudocilia; *B*, division of cells to form gametes; *C*, gamete greatly enlarged (note similarity to *Chlamydomonas* in two contractile vacuoles, eyespot, and cup-shaped chloroplast with single pyrenoid); *D–F*, stages in fusion of gametes; *G*, young zygote; *H*, mature zygote; *I*, two groups of aplanospores, each formed by the germination of a single zygote; *J*, young colony formed by the germination of a group of aplanospores. All except *D*, *T. gelatinosa* (after Klyver); *D*, *T. lubrica* (after Reinke). (All except *C* and *D*, × 650)

Palmella is of great interest because it has a dominant phase consisting of a colony of non-motile cells in which repeated vegetative divisions result in a large number of vegetative cells. These features are characteristic of most of the *Tetrasporales* and are generally interpreted as indicating the beginning of a line of evolution which has resulted in the large stationary vegetative bodies of higher plants. The *Volvocales* represent the evolution of the motile phase of such primitive algae as *Chlamydomonas*. This line of evolution is known as the volvocine line, and any series of forms showing the evolution of motile colonies is said to show a volvocine tendency. In a similar way the *Tetrasporales* represent the development of palmelloid colonies and indicate the beginning of a line of evolution in which motility is restricted to reproductive stages and in which there is a development of vegetative divisions of non-motile cells with the production of non-motile vegetative cells. This line of evolution is called the tetrasporine line, and any series in which the above characteristics are prominent is said to show a tetrasporine tendency. Series with volvocine and with tetrasporine tendencies are found in other divisions of algae besides the *Chlorophyta*.

Tetraspora. This genus is very like *Palmella* except that the individual cells have two long motionless protoplasmic processes, or pseudocilia, on the side toward the exterior of the colony (Fig. 484). These pseudocilia extend to or beyond the boundary of the colony. Different species have irregular gelatinous colonies of various sizes and shapes. *Tetraspora* resembles *Palmella* in that non-motile vegetative cells readily change to biflagellate motile cells which swim out of the parent colony and start a new colony. When a non-motile cell becomes motile the pseudocilia are discarded and true flagella produced. Also, as in *Palmella*, biflagellate zoospores are formed by the division of the protoplast of a non-motile vegetative cell, and sexual reproduction is due to the fusion of biflagellate isogametes.

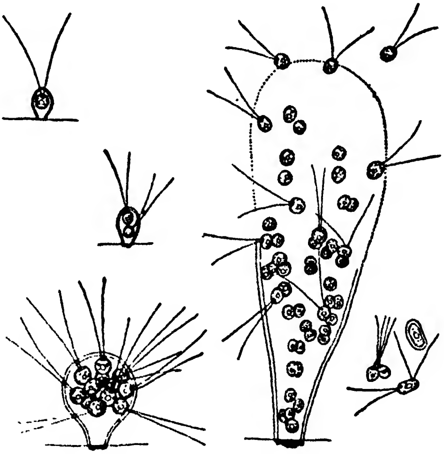


FIG. 485. *Apiocystis brauniana*

Left, stages in development of colony; center, zoospores escaping from the colony; right, fusion of gametes to form zygote. (× 300). After Moore

Apiocystis. This alga forms microscopic pear-shaped colonies which are attached to some object by the small end (Fig. 485). The cells are arranged near the periphery of the colony, and each has two pseudocilia which project from the gelatinous envelope of the colony. As in *Palmella* and *Tetraspora*, non-motile vegetative cells may change to motile ones and leave the colony, biflagellate zoospores are formed by the division of the protoplast of a vegetative cell, and sexual reproduction takes place by the fusion of small biflagellate isogametes.

Prasinocladus. The genus *Prasinocladus* is an interesting member of the *Tetrasporales* because it forms branched colonies, often called dendroid colonies (Fig. 486). Perhaps the chief interest in this curious type of colony lies in the fact that dendroid colonies are found in other lines of evolution which parallel more or less the evolution in the green algae. A colony is started by a quadriflagellate zoospore which settles on some substratum, loses its flagella, and secretes a gelatinous envelope. After a time the outer layer of the envelope may rupture at the apex and the contents move outward and partially escape. After this partial escape the protoplast forms additional enveloping material. When the protoplast which moves upward divides into two, branching results. At times the migrating protoplast is flagellated, and the protoplast may escape as a quadriflagellate zoospore and swim away to form a new colony. A relationship to the very primitive green algae is indicated by the presence of an eyespot and a cup-shaped chloroplast with a single pyrenoid. At the anterior end of the cell there is a contractile vacuole.

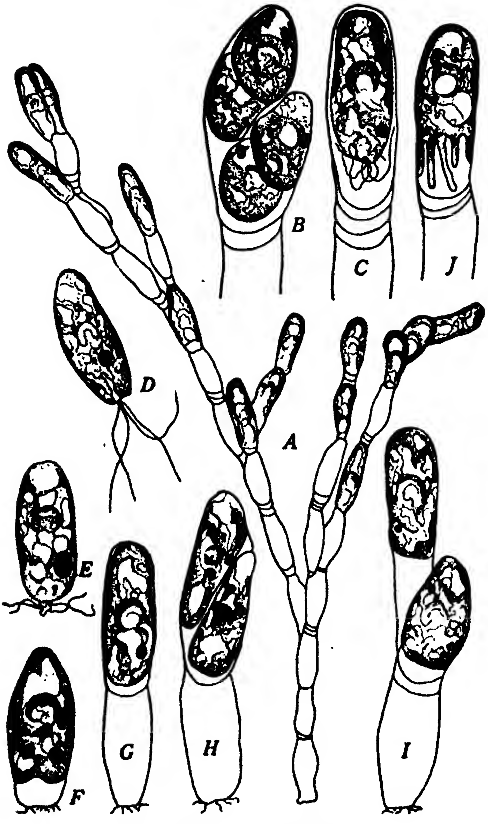


FIG. 486. *Prasinocladus*

A, habit of colony (× 220); *B*, end of a branch in which one cell has given rise to four; *C*, a zoospore at the end of a branch; *D*, zoospore; *E–I*, germination of zoospore to produce a colony; *J*, tip of a branch at the time the terminal cell is moving forward. (After Davis)

ORDER *ULOTRICHALES*, FILAMENTOUS AND EXPANDED GREEN ALGAE

Ulothrix, a Simple Filamentous Green Alga

General characteristics. *Ulothrix* is a filamentous green alga which is frequently abundant as a hairy covering on stones in slow-running streams, ponds, etc. The plant consists of a single unbranched row of cells (Fig. 487). The cells are all similar and capable of division and reproduction, except the basal one which serves to attach the plant to the substratum. Each cell contains a single nucleus and a single chloroplast (Fig. 487). A filament increases in length by transverse divisions of the cells.

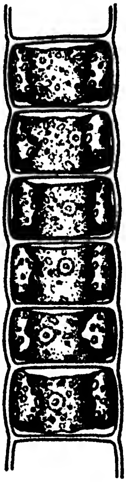


Fig. 487. Cells from filament of *Ulothrix*

Note that each cell contains a single nucleus and a band-shaped chloroplast. (× 462)

When a cell divides, the protoplast divides into two daughter protoplasts as in *Chlamydomonas* (Fig. 488). These daughter protoplasts are separated from each other by the formation of a cross wall which divides the mother cell in two. Except for this cross wall, the daughter cells are surrounded by the walls of the mother cell. The separation of daughter protoplasts by the formation of a cross wall is similar to what we find in higher plants and is in striking contrast to the type of wall formation characteristic of *Chlamydomonas* and the motile colonies related to it. We have seen that in these cases walls are formed anew around the entire protoplasts of the daughter cells and that the wall of the mother cell disintegrates. In *Ulothrix* a new wall is formed only between the two daughter protoplasts, and this results in the production of a cross wall which is attached to the persistent walls of the mother cell. The division of a cell into two parts by the formation of a cross wall enables *Ulothrix* to form filaments. *Ulothrix* is filamentous because partition walls are formed in only one direction; that is, transverse to the mother cell. The same type of wall formation in two planes results in sheets. Wall formation in three directions builds solid tissue.

Asexual reproduction of *Ulothrix*. Asexual reproduction takes place by means of zoospores with four flagella (Fig. 489). These zoospores are similar to those of *Chlamydomonas* and the *Tetrasporales*, and each contains a red eyespot and a chloroplast. The zoospores are formed from ordinary vegetative cells by the division of the protoplast into a number of separate parts, each of which acquires the characteristics of a zoospore. This method of formation is the same as we have observed in zoospore formation in *Chlamydomonas*. The zoospores escape through an opening in the cell wall, and, after swimming for a time, come to rest and grow into new plants (Fig. 489). In germinating, a zoospore elongates and is divided into two cells by a transverse division. Repeated transverse division of the cells results in the production of a mature plant.

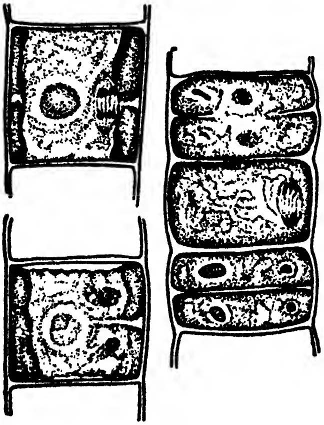


Fig. 488. ***Ulothrix***

Stages in division of protoplasm by cleavage. Note nuclei dividing by mitosis. (After Lind)

Sexual reproduction. *Ulothrix* reproduces sexually by means of biflagellate gametes. They are produced in the same way as the zoospores. In structure they are like the zoospores except that the gametes never possess more than two flagella, are smaller than zoospores, and are produced in much larger numbers in a cell (Fig. 489). Two gametes fuse to form a single cell known as a zygospore (Fig. 489), which becomes surrounded by a cell wall. After a period of rest, the zygospore germinates and produces a small single-cell plant. The protoplast of this divides to form a number of zoospores which, like other zoospores, grow into ordinary vegetative plants (Fig. 489).

The fact that gametes are similar to zoospores indicates, as in *Chlamydomonas*, that gametes are modified zoospores and that sexuality may have resulted in some ancestor of *Ulothrix* through a change of non-sexual zoospores into sexual gametes.

In the same species of *Ulothrix* there may be a fusion of isogametes, in which case there is no distinction of sex, or there may be a fusion of microgametes (small gametes) and megagametes (large gametes) which indicates an early stage in the differentiation of sexes.

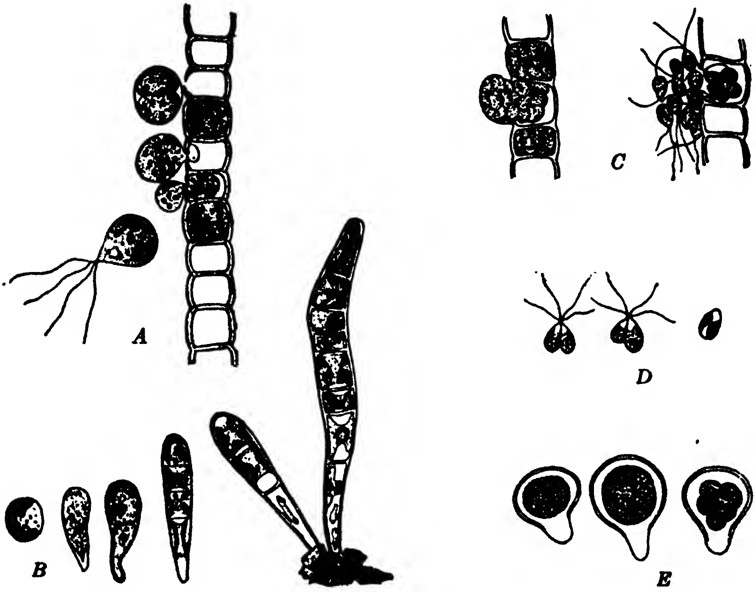


FIG. 489. *Ulothrix*

A, the formation of zoospores; *B*, the germination of zoospores; *C*, the formation and escape of gametes; *D*, the conjugation of gametes; *E*, the germination of zygospore with the production of zoospores. (Redrawn after Dodel-Port)

Relationship of *Ulothrix*. The similarity of reproductive cells of *Ulothrix* to the mature individuals, the zoospores, and the gametes of *Chlamydomonas* and to the motile reproductive cells of the *Tetrasporales* indicates that *Ulothrix* may have been derived from some such form as *Chlamydomonas* through the *Tetrasporales*. Not only are reproductive cells of *Ulothrix* similar to those of *Chlamydomonas*, but the method of division by which they are formed is also similar.

The great advance shown by *Ulothrix* over the *Tetrasporales* is that when daughter protoplasts are produced by vegetative divisions, the only new walls formed are cross walls which serve to hold the daughter cells together. This results in the production of a filamentous plant body. The chief difference between the *Tetrasporales* and *Ulothrix* is thus in vegetative structure rather than in the methods of reproduction. There are, however, genera with vegetative forms intermediate between the irregular gelatinous colonies of such types as *Palmella* and the filaments of *Ulothrix*. These intermediate forms may suggest the course followed by the ancestors of *Ulothrix*. One of these is shown in Fig. 490.

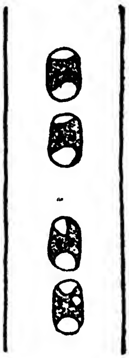


Fig. 490. *Geminella interrupta.* (× 480)
After Lagerheim

In *Ulothrix* cell division is always in the same plane; but in some advanced green algae division in more than one plane results in various types of branched filaments and sheets. The same method of division makes possible the complicated types of plant body which we find in flowering plants.

✓ In *Ulothrix* we see the two prominent characteristics of the tetrasporine line. The non-motile phase is dominant, with motility confined to reproductive cells, and there is a considerable development of vegetative divisions. Thus *Ulothrix*, its relatives, and their descendants represent a continuation of the tetrasporine line of evolution.✓

Various *Ulotrichales*

General characteristics. *Ulothrix* is a very primitive representative of a large order of green algae, the *Ulotrichales*. The most primitive of the *Ulotrichales* are unbranched filaments. Some forms are simple branched filaments; others have a complicated branching system consisting of a prostrate creeping part from which erect branches arise; still others are in sheets which in places may be several cells in thickness. In the order we find sexual reproduction by the fusion of isogametes, the fusion of heterogametes (gametes of different sizes), and the fertilization of eggs by spermatozoids. Asexual reproduction takes place in various ways, including the fragmentation of the plant body and the formation of zoospores and of aplanospores and akinetes. Aplanospores are thick-walled spores which are formed within a vegetative cell and are surrounded by a wall which is distinct from that of the cell in which it is contained. An akinete is a thick-walled spore in the formation of which an entire vegetative cell, including the cell wall, takes part.

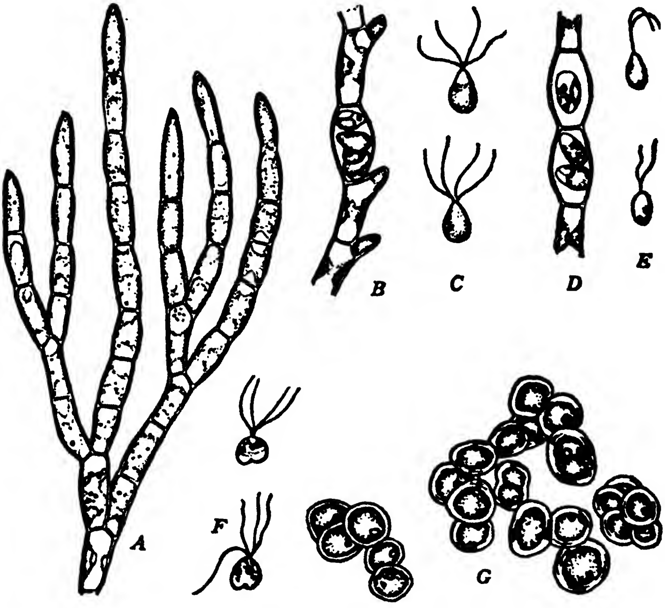


FIG. 491. *Stigeoclonium flagelliferum*

A, branches in a fairly young stage; *B*, zoosporangium with zoospores; *C*, zoospores; *D*, gametangia with gametes; *E*, gametes; *F*, fusion of gametes; *G*, palmella stage. (× 300). After Tilden

Stigeoclonium. *Stigeoclonium* is a filamentous alga with a cushionlike basal portion from which spring numerous rather sparingly branched erect filaments (Fig. 491). The cells have many points in common with those of *Ulothrix.* Asexual reproduction is by means of zoospores which develop from vegetative cells. Vegetative reproduction is also due to aplanospores and akinetes. Sexual reproduction is by the fusion of biflagellate isogametes. *Stigeoclonium* often changes to a palmella stage, in which it multiplies vegetatively. The presence of this palmella stage and the similarity of the reproductive cells to those of *Chlamydomonas* indicate that, just as in the case of *Ulothrix*, *Stigeoclonium* was derived through the *Tetrasporales* from some form resembling *Chlamydomonas*.

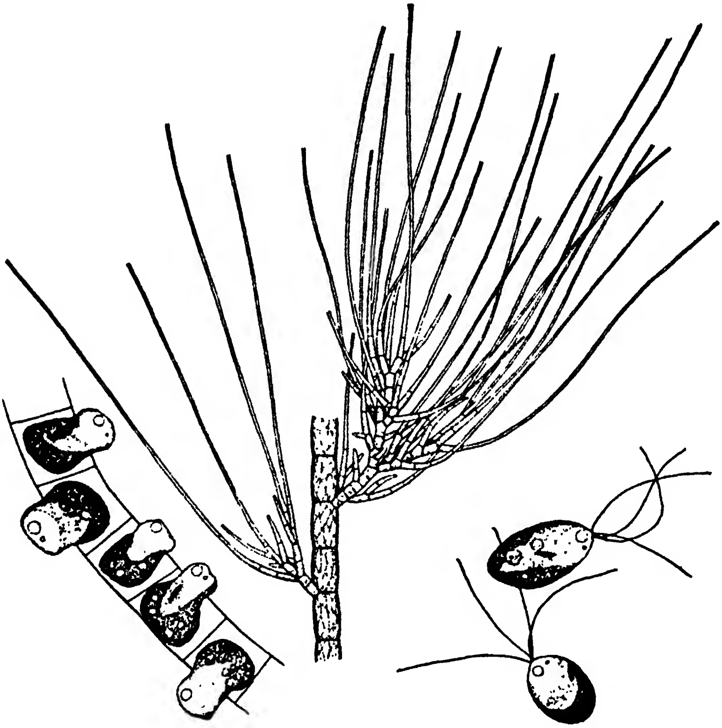


FIG. 492. *Draparnaldia*

Center, method of branching (× 65); lower left, escape of zoospores; lower right, zoospores. Note two contractile vacuoles, eyespot, and cup-shaped chloroplast. (Lower figures after Johnson)

Draparnaldia. Species of *Draparnaldia* are like *Stigeoclonium* in having prostrate and erect parts. In the erect part there is a conspicuous differentiation between large main branches and smaller side branches (Fig. 492). Asexual reproduction is by quadriflagellate zoospores which are formed in the cells of the small branches (Fig. 492). A zoospore has a single chloroplast with one or more pyrenoids, an eyespot, and two contractile vacuoles which contract alternately. The zoospores, therefore, have characteristics which are very similar to those of the most primitive green algae. Although *Draparnaldia* shows a very high degree of vegetative differentiation, it indicates the character of the primitive green algae from which it appears to have been derived when it produces zoospores. *Draparnaldia* reproduces sexually by the fusion of quadriflagellate gametes.

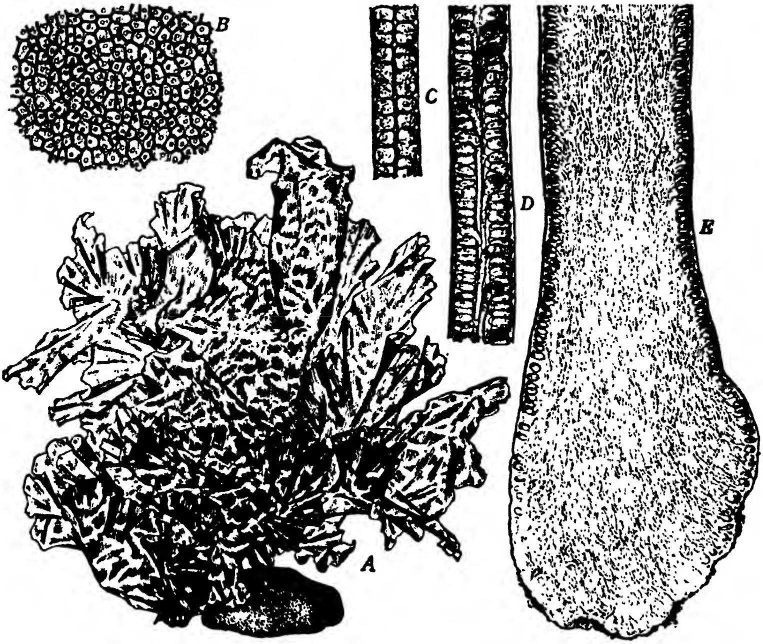


FIG. 493. *Ulva lactuca*

A, habit of young plant; *B*, surface view of vegetative portion, showing cellular structure; *C*, cross section; *D*, longitudinal section where cells are beginning to form tubular filaments; *E*, section of base showing holdfasts composed of filaments formed by outgrowths of cells. (*A*, × ½; *B–E*, × 150). After Thuret

Ulva. *Ulva* is a marine alga which consists of a large sheet two cells in thickness and frequently several meters in length (Fig. 493). Asexual reproduction is by means of zoospores (Fig. 494). These are formed in ordinary vegetative cells by the dividing up of the protoplast and the metamorphosis of the divided parts into zoospores, which escape through an opening in the cell wall. Sexual

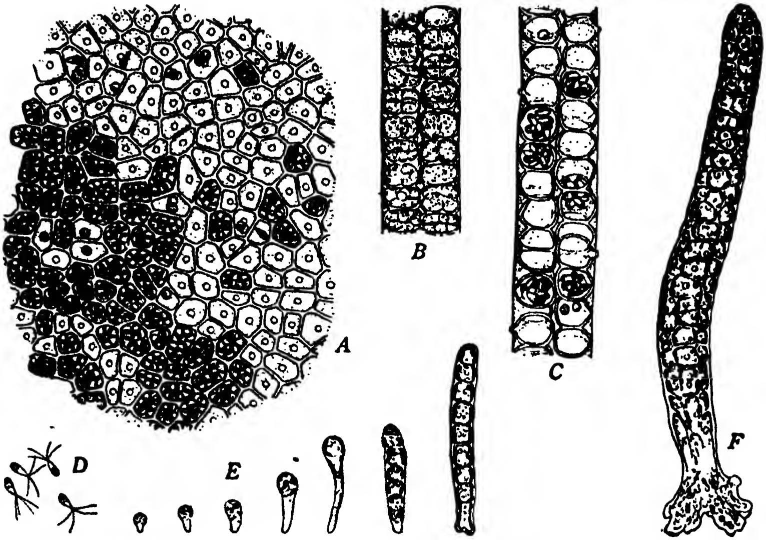


Fig. 494. *Ulva lactuca*

A, surface view of cells forming zoospores; *B*, longitudinal section showing cells forming zoospores; *C*, mature zoospores in cells; *D*, zoospores; *E*, *F*, germination of zoospores. (*A–D*, × 220; *E*, *F*, × 110). After Thuret

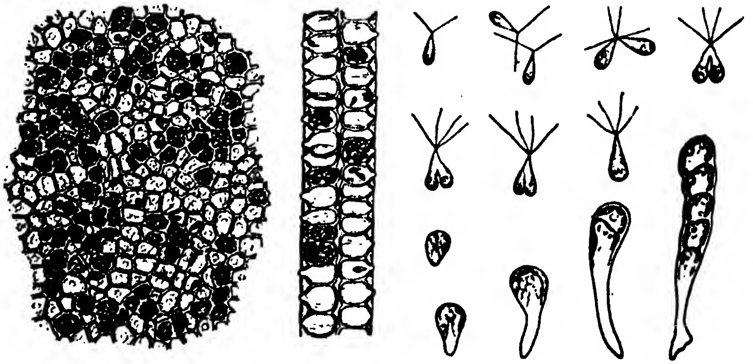


Fig. 495. *Ulva lactuca*

Left, surface view of cells forming gametes; center, section through cells containing gametes and others from which gametes have escaped (× 200). Upper right, gametes and fusion of gametes; lower right, germination of zygote (× 450). After Thuret and Borzi reproduction is by means of biflagellate isogametes, which are formed from vegetative cells in much the same way as are the zoospores (Fig. 495).

Two gametes fuse to form a zygote, which germinates immediately to give rise to a thallus that produces only zoospores. These in turn give rise to thalli that produce only gametes and not zoospores. Thus in the life history of *Ulva* there is an alternation of plants which reproduce asexually by means of zoospores and plants which form gametes and not zoospores. The asexual and sexual plants look alike, and so we cannot tell them apart except when they are producing reproductive cells.

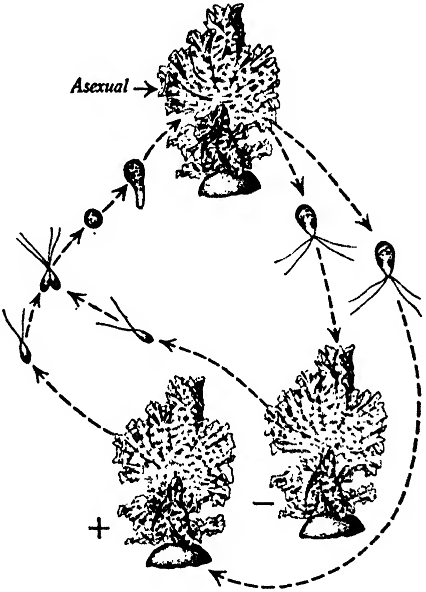


Fig. 496. **Diagram showing alternation of generations in life history of *Ulva lactuca***

Above is an asexual plant. Below are the two kinds of sexual plants which are designated + and − . The zoospores from the asexual plant give rise to sexual plants. These produce gametes which fuse to form a zygote the germination of which results in an asexual plant

The sexual plants have a single or haploid number of chromosomes, while the asexual ones have a double or diploid number. As the gametes are derived from sexual plants with the haploid number of chromosomes, the gametes also have the haploid number. When two gametes fuse, the resulting zygote has the diploid number. A zygote, on germination, gives rise to an asexual thallus with the same number of chromosomes as the zygote (diploid). When these plants produce zoospores the number of chromosomes is reduced so that the zoospores have a haploid number and give rise to sexual plants with a haploid number. There is thus an alternation not only of asexual and sexual plants, but of asexual plants with a diploid number of chromosomes and sexual plants with a haploid number. This alternation is known as the *alternation of generations*; that is, an alternation of a diploid asexual generation and a haploid sexual one. This alternation of generations is a very important feature in botanical studies, as it is characteristic of most brown and red algae and of bryophytes and all higher plants.

In *Ulva* all the gametes look alike, so that we can hardly speak of male and female gametes. However, there are really two kinds of sexual plants, although they look alike and produce gametes that look alike. This is shown by the gametes in fusing. Gametes from the same thallus or from thalli of the same kind will not fuse with each other, while those from different kinds will fuse. There is thus an alternation of an asexual plant and two kinds of sexual ones (Fig. 496). This condition is general in algae with an alternation of generations.

The basal portion, or holdfast, of *Ulva* is differentiated in a very peculiar manner. The cells of the lower part of the thallus produce tubular outgrowths which grow downward between the two layers of cells of the thallus (Fig. 493). These outgrowths of the cells are interlaced and make the lower portion of the thallus strong. Near the base they emerge and form a stout holdfast.

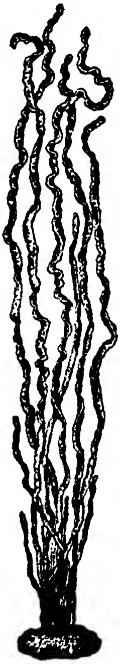


Fig. 497. ***Enteromorpha intestinalis*, a relative of *Ulva*.** (× ½)

Related to *Ulva* is the genus *Enteromorpha* (Fig. 497). The thallus is a hollow tube with a wall one cell in thickness. This tube is formed by the separation of two layers such as we see in *Ulva*. In *Enteromorpha*, as in *Ulva*, all plants are alike, but there is an alternation of asexual plants reproducing by zoospores and sexual plants producing gametes. In those species which have been studied, the gametes of a fusing pair, as we have seen to be the case in *Ulva*, come from different plants. In one species of *Enteromorpha* the gametes which fuse with each other are heterogametes (Fig. 498); that is, one is large and the other is small, indicating a differentiation of sex. Here we again see the tendency of various lines of algae to develop a differentiation of sex.

Relationship of *Ulva*. Although *Ulva* is a much larger plant than *Ulothrix*, the similarity of the cells and particularly of the gametes and zoospores in the two indicates that they are related, and that *Ulva* is simply a more advanced form of *Ulothrix*. The difference between the structure of the plant body of *Ulothrix* and of *Ulva* and its relatives is, however, so great that some botanists prefer to place *Ulva* and its relatives in a separate order, the *Ulvales*.

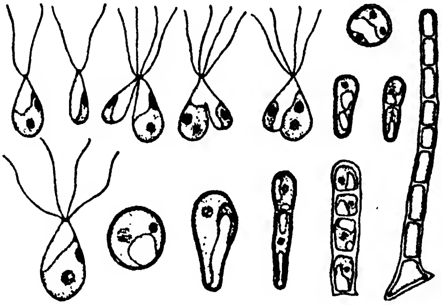


FIG. 498. *Enteromorpha intestinalis*

Upper line, large and small gametes, their fusion to form a zygote, and the germination of the zygote. Note conspicuous eyespot and the pyrenoid in the chloroplast. Lower line, zoospore and its germination. (Gametes and zoospore, × 1250). After Kylin

Coleochaete

General characteristics. *Coleochaete* is a small alga that usually grows epiphytically on other water plants. It is of great interest because of the fact that it exhibits highly developed oogamy, as it has large non-motile eggs which are fertilized by small motile spermatozoids. *Coleochaete* consists of branching filaments. In some species all the filaments are prostrate and radiate from a center (Fig. 499). These filaments are often so close together as to form a continuous sheet. Asexual reproduction is by means of biflagellate zoospores which are formed singly within a cell (Fig. 500).

Sexual reproduction. The eggs of *Coleochaete* are borne singly in special cells or oogonia (Figs. 499, 501) which are formed by end cells of branches. In one species a long slender projection called a trichogyne projects from the oogonium (Fig. 501, 502). In other species the projection is at most a small papilla. After the formation of an oogonium the vegetative cells continue to grow, so that in disk forms of *Coleochaete* the oogonium soon comes to be well within the margin of the disk (Fig. 499).

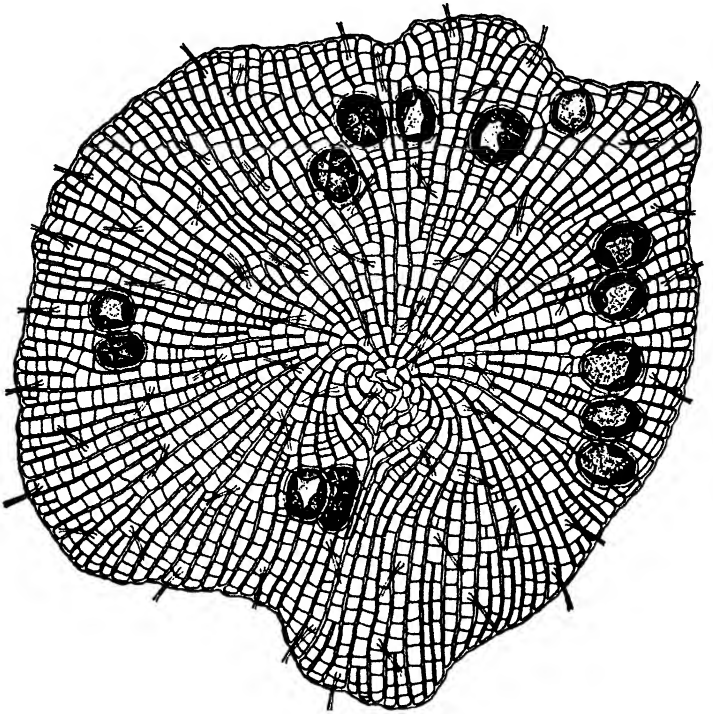


FIG. 499. A disk form of *Coleochaete*

Note that it is composed of branching filaments which are so close together as to produce the appearance of a solid sheet. The dark bodies are fertilized eggs. These are overgrown to various extents by surrounding cells. (× 150)

The spermatozoids are biflagellate, and are formed singly in small specialized cells, the antheridia (Fig. 502). In disk forms the antheridia are produced by the division of vegetative cells (Fig. 503).

After leaving an antheridium, a spermatozoid swims around. If it reaches an oogonium, it may enter through an opening produced by the gelatinization of the wall at the tip of the papilla or trichogyne. The fertilized egg enlarges considerably and becomes surrounded by a thick wall to form an oospore. During the growth of the oospore, branches from the cell at the base of the oogonium and from the surrounding cells grow up over the oogonium and form a sterile covering around it (Figs. 499, 501, 502). The oospore is very resistant to adverse conditions, and may remain throughout the winter season without germinating. On germination, the contents divide up to form sixteen or thirty-two cells (Fig. 501), within each of which a zoospore is produced.

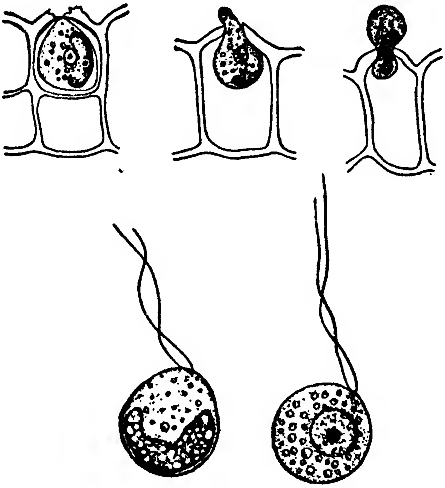


FIG. 500. *Coleochaete*

Upper line, escape of zoospores (× 340). Lower left, zoospore drawn to show chloroplast; lower right, zoospore drawn to show nucleus and not chloroplast (× 900). After Wesley

The thallus of *Coleochaete* has the haploid number of chromosomes. When an egg is fertilized by a spermatozoid the diploid number results. This number is reduced and the condition becomes haploid during the first two divisions of the germinating oospore, so that during the further development of the cell mass which results from the germination of the oospore there is a haploid number of chromosomes. In *Coleochaete* there is, then, nothing which can be interpreted as an alternation of a haploid sexual generation and a diploid asexual one. In *Coleochaete* there is an alternation of a sexual generation producing eggs and spermatozoids and the development of an asexual cellular mass with the production of zoospores. This cannot, however, be interpreted as a true alternation of generations.

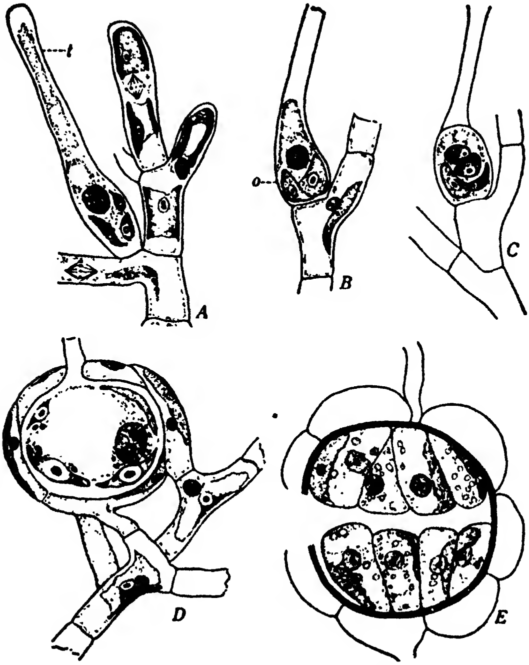


Fig. 501. *Coleochaete pulvinata*

A, portion of a plant showing oogonium with trichogyne (*t*); *B*, the trichogyne of the oogonium (*o*) has opened; *C*, male and female nuclei are together in the oogonium; *D*, section of fertilized oogonium surrounded by cells produced by neighboring filaments; *E*, section of cellular mass formed by germinating of oospore. (After Oltmanns)

Coleochaete is a member of the *Ulotrichales*, and shows a high differentiation in sexual reproduction. In most of the *Ulotrichales* sexual reproduction is due to the fusion of isogametes, but heterogametes are also known (Fig. 498). We find, therefore, that in the *Ulotrichales*, just as in the *Volvocales*, there are various stages in the differentiation of sex. As far as we can tell, the oogamy of *Volvox* and that of *Coleochaete* were developed entirely inde-

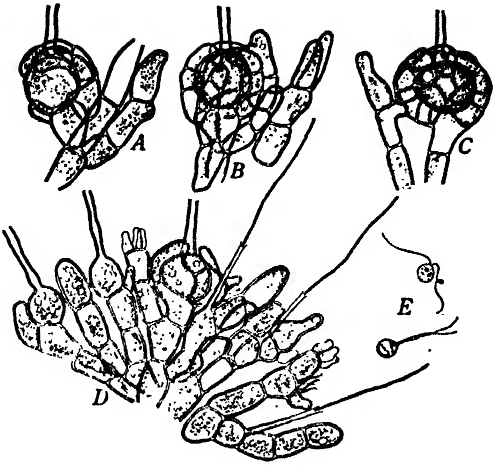


Fig. 502. *Coleochaete pulvinata*

D, portion of a plant, showing oogonium in various stages of development and also antheridia, which are the small cells at the ends of filaments; *A*, *B*, *C*, growth of neighboring filaments around the oospore; *E*, spermatozoids. (After Pringsheim)

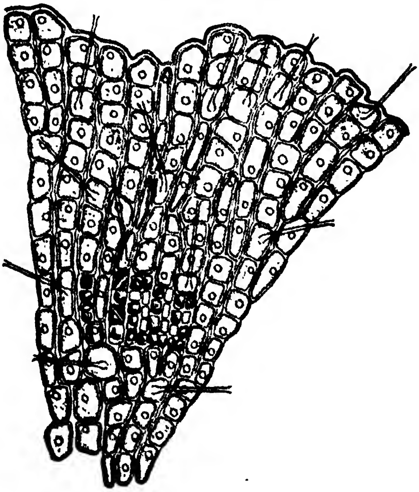


Fig. 503. *Coleochaete scutata*

Portion of a plant showing antheridia from some of which the spermatozoids have escaped. The antheridia are the small cells below the center of the drawing. (After Pringsheim) pendently: for *Volvox* is the culmination of the volvocine line of evolution, while *Coleochaete* represents a high degree of sexual differentiation in the tetrasporine line. These are by no means the only cases of the independent development of oogamy. In fact, it appears that such a development has taken place many times in the plant kingdom.

Protococcus

General characteristics. *Protococcus* is one of the commonest, if not the most common, of all green algae, and is one of the most widely distributed and most numerous of all plants. It [illegible] a very simple plant, perhaps the simplest of all green algae (Fig. 504). Students of the algae, however, are generally agreed that the simplicity of *Protococcus* is due to its being a reduced rather than a primitive form. An individual *Protococcus* is either a single cell or a thallus of a few cells; that is, two or three or four and sometimes a few more. Each cell has a nucleus and a single chloroplast. The cells readily separate from each other. *Protococcus* is often found as a green coating on damp places, particularly on trees, stones, walls, etc. The only method of reproduction known in *Protococcus* is the division of one cell into two and the separation of the resulting cells.

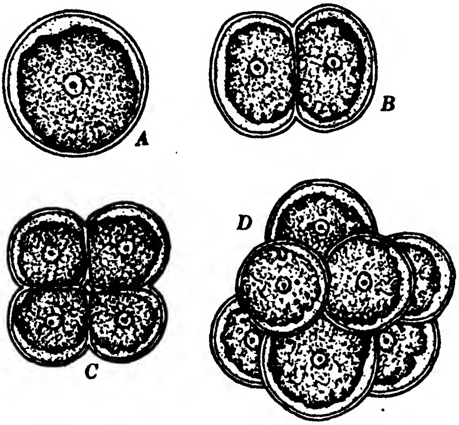


Fig. 504. *Protococcus*, a green alga which is common as a green coating on tree trunks and stone walls. (× 2470)

A, a single cell; *B*, a plant consisting of two cells; *C*, a plant composed of four cells; *D*, a group of separate cells. Note the large chloroplast in each cell

Neither sexual reproduction, motile cells, nor any special form of reproduction is known in *Protococcus*. That this condition is not primitive is indicated by many facts. Motility is characteristic of the flagellates, from which green algae appear to be descended. The most primitive green algae, of which *Chlamydomonas* may be regarded as a type and from which radiate various lines of evolution, are characterized by motility and sexuality. Moreover, the method of cell division in *Protococcus* is not primitive. In the most primitive green algae division is not due to the formation of a cross wall but to the division of the protoplast itself; each daughter protoplast then surrounds itself with a new wall, and the wall of the mother cell disintegrates. The more specialized type of cell division that we have in the vegetative divisions of the *Ulotrichales* is characterized by the formation of a cross wall across the cell. It is this method of cell division by cross-wall formation that we find in *Protococcus*. The most primitive algae are unicellular, while

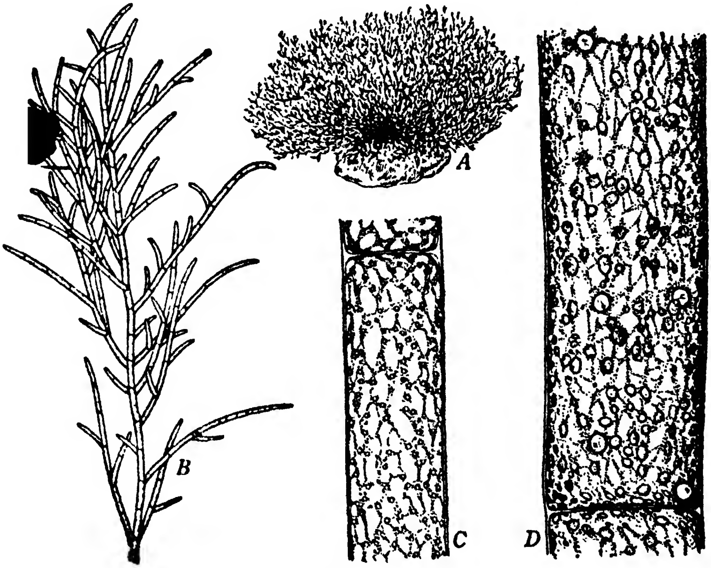


FIG. 505. *Cladophora*

A, habit (× ⅖). *B*, portion of a plant (× 6). *C*, portion of chloroplast in very young cell; note that it is reticulate with many pyrenoids. *D*, portion of mature cell; five nuclei, which are the large light-colored structures, are visible. The pyrenoids, which are mostly oval and are shown as darker than the nuclei, are very numerous

Protococcus shows relationship to the *Ulotrichales* by the fact that it may be multicellular owing to the formation of cross walls. Moreover, these walls are not confined to one plane as in *Ulothrix* but are formed in different planes, a characteristic of the more highly developed *Ulotrichales.*

Protococcus affords a good example of the fact that evolution does not always proceed toward complexity. As it shows cross-wall formation in more than one plane, it seems that it mus[illegible]e descended from some fairly complex member of the *Ulotrichales*, and that therefore its ancestors had sexual reproduction and had also asexual reproduction by means of zoospores. The simplicity of *Protococcus* may be connected with its change to a terrestrial habitat. Certainly, delicate branched algae could not survive in situations where *Protococcus* grows. If success is to be judged by the existence of enormous numbers of individuals over a large part of the earth, then *Protococcus* is an exceedingly successful alga.

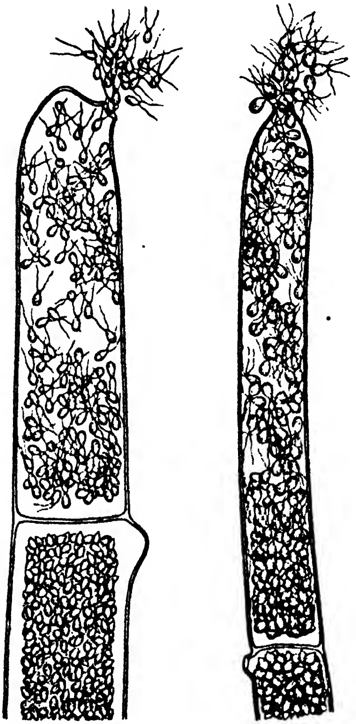


Fig. 506. ***Cladophora***

Left, gametangia with biflagellate gametes; right, zoosporangia with quadriflagellate zoospores

Cladophora

The thallus of *Cladophora* is a branching filament in which the cells are very long in shape (Fig. 505). Asexual reproduction is by means of quadriflagellate zoospores (Fig. 506). Sexual reproduction is by the fusion of biflagellate isogametes (Fig. 506). Both zoospores and gametes are formed by the division of the contents of vegetative cells. *Cladophora* is of interest because each cell contains many nuclei, and also because there is an alternation of generations in its life history. Both generations are alike in appearance, but one produces zoospores and the other gametes. The

zoospores are produced by a plant of the asexual generation. On germination they give rise to sexual plants, which produce gametes. The gametes fuse to form a zygote, which on germination gives rise to an asexual plant, thus completing the alternation of generations. In some species it is evident that, as in *Ulva*, there are two kinds of gametophytic plants, because gametes from one plant will not fuse with gametes from the same plant but only with gametes from a different individual. It seems likely that an alternation of generations has arisen independently many times in the plant kingdom, and that the alternation of generations in *Cladophora* arose independently of that in *Ulva*.

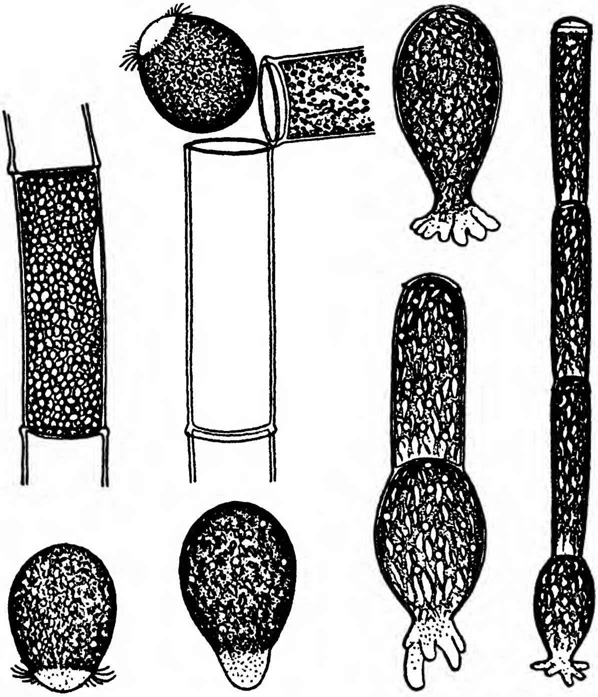


Fig. 507. *Oedogonium*

Formation and escape of zoospore and germination of zoospore resulting in a young plant. Note reticulate character of chloroplast in young plants

ORDER *OEDOGONIALES*

Oedogonium

General characteristics. *Oedogonium* is a very common and widely distributed alga, and is an excellent example to illustrate highly developed sexual reproduction in which a large non-motile egg is fertilized by a small motile spermatozoid. For these reasons *Oedogonium* is a classic example of oogamous reproduction. The *Oedogonium* plant consists of an unbranched filament which, when young, is attached to the substratum by a basal cell developed as a holdfast (Fig. 507). When the filaments become older they may float freely in the water (Fig. 508). Each cell contains a single nucleus and a single large chloroplast, which is near the wall and completely encircles the more central portion of the cell contents. The chloroplast is reticulate and composed of anastomosing strands (Figs. 507, 508). The chloroplast has many pyrenoids, which are located at the points where the strands join each other. Starch is formed around the pyrenoids (Fig. 509).

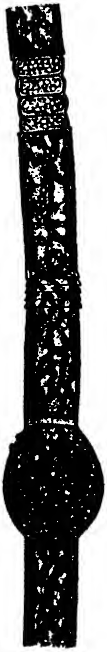


FIG. 508. Filament of *Oedogonium*

Below is a large rounded oogonium, and above are four small cells, the antheridia. (×240)

Cell division. The method by which the cells of *Oedogonium* divide is very different from that seen in any other known plant except in two closely related genera (Fig. 509). In *Oedogonium*, before division, the nucleus migrates toward the apical end of the cell. During the early stages of division a ring, generally believed to be of hemicellulose, appears on the inner surface of the cell wall near the apical end (Fig. 509 *B*). Soon a groove appears in this ring where the ring touches the cell wall. On either side of the groove the ring remains joined to the cell wall of the mother cell, and the ring enlarges (Fig. 509 *C*). Meanwhile the nucleus has divided. The division of the nucleus is followed by a transverse division of the protoplast (Fig. 509 *E*). The mother cell wall now ruptures opposite the groove, and the ring stretches out (Fig. 509 *F*). The two daughter protoplasts elongate until the lower one occupies approximately that portion of the cell which is surrounded by the old wall of the mother cell while the upper protoplast fills that portion surrounded by the wall formed from the elongation of the ring and the very small portion of the mother cell which was above the ring (Fig. 509 *G*). This portion is plainly seen as a cap at the apex of the cell. When an apical end has taken part in several divisions it is surrounded by a series of ringlike markings around the tip, each ring being formed by a different division. The two daughter protoplasts resulting from the division of a single cell are finally separated from each other by the secretion of a cell wall. This is joined to the mother cell wall at approximately the place where the lower part of the wall of the mother cell joins the wall formed by the stretching of the ring.

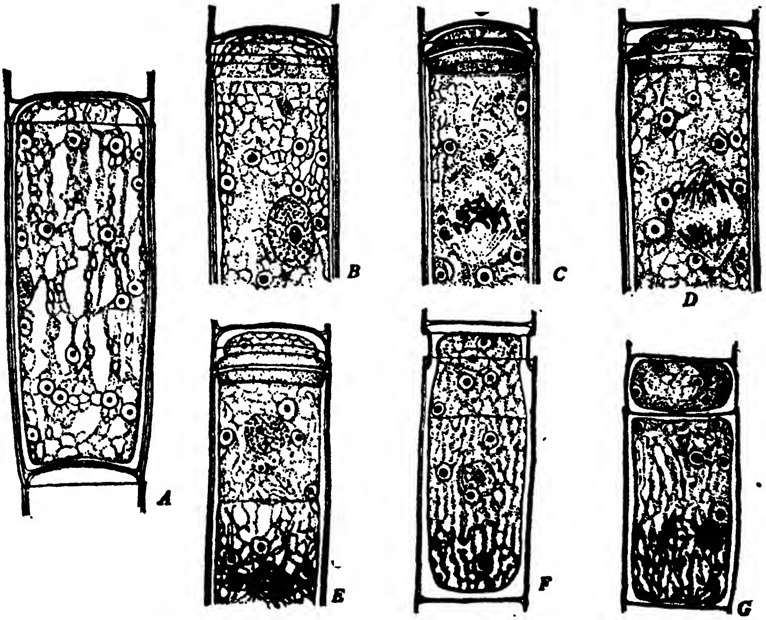


FIG. 509. ***Oedogonium***

A, vegetative cells, showing character of protoplast with pyrenoids; *B*–*G* successive stages in cell division. (× 600). After Ahashi

Asexual reproduction. Asexual reproduction is by zoospores, which are formed singly in vegetative cells (Fig. 507). The zoospores are egg-shaped structures. The anterior region is clear and

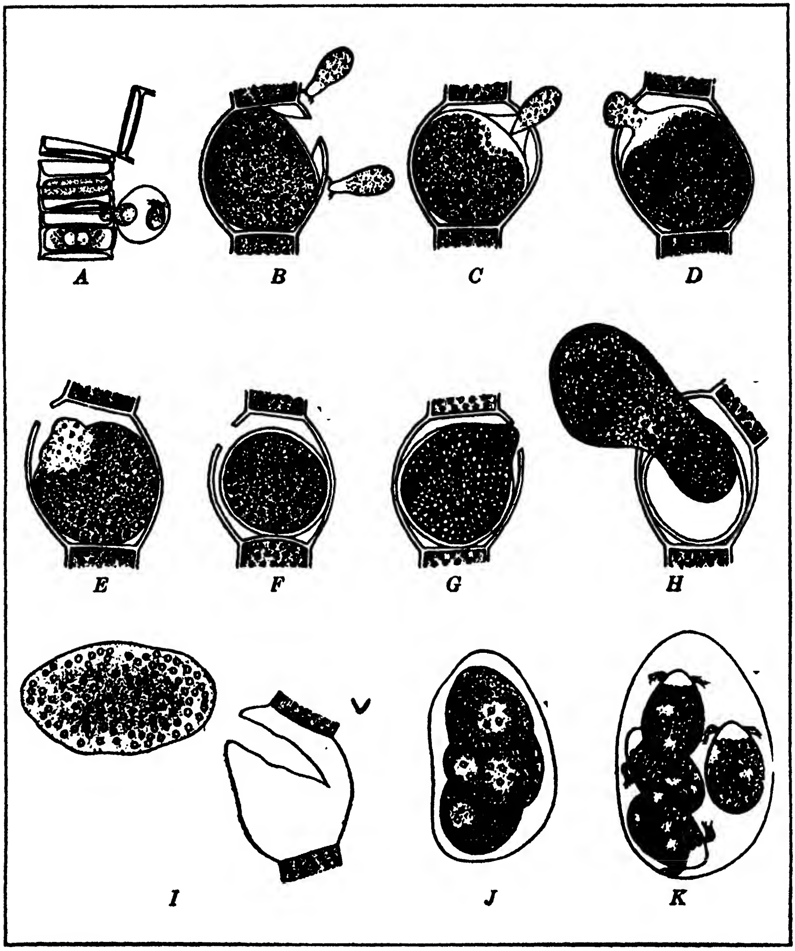


FIG. 510. *Oedogonium*

A represents the escape of spermatozoids; *B–E*, fertilization; *F*, oospore; *G–I*, escape of contents of oospore; *J*, *K*, formation of zoospores. (*A* redrawn after Hirn; the remainder redrawn after Juranyi) is surrounded by a circle of flagella, while the remainder of the zoospore is colorêd green by the chloroplast. The zoospore sometimes contains an eyespot. The zoospore is liberated by the transverse rupture of the cell near its anterior end. When the zoospore leaves the cell it is surrounded by a delicate vesicle, which soon disappears. The zoospore swims about for a while, then attaches itself to some object by means of its anterior end, withdraws its flagella, produces a cell wall, and grows into a new filament (Fig. 507).

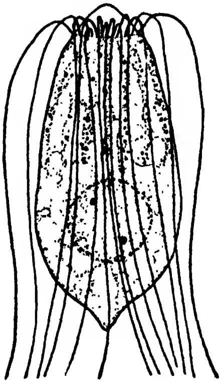


Fig. 511. Spermatozoid of *Oedogonium kurzii*

Note reticulate chloroplast in anterior portion and large rounded nucleus in posterior region. (× 1200). After Spessard

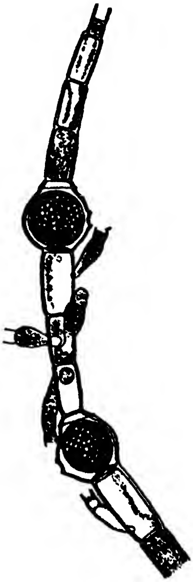


Fig. 512. Plant of *Oedogonium* with two rounded oogonia and five dwarf males attached to it

Redrawn after Pringsheim

Sexual reproduction. Sexual reproduction is the result of a fertilization of a large non-motile egg by a flagellated spermatozoid (Fig. 510). The eggs are borne singly in oogonia. The oogonium of *Oedogonium* is a large rounded cell. The spermatozoids are borne in antheridia, which in *Oedogonium* are small cells which occur in rows (Fig. 508). Usually each antheridium forms two spermatozoids. These are similar to the zoospores except that they are smaller. Like the zoospores, they have a circle of flagella (Fig. 511); and, again like the zoospores, they are surrounded by a delicate evanescent vesicle. When they leave the antheridium they are set free by transverse rupture of the cell wall just as are the zoospores. When the egg is ready for fertilization, an opening appears in the wall of the oogonium. It is through this opening that the spermatozoid can enter the oogonium and fertilize the

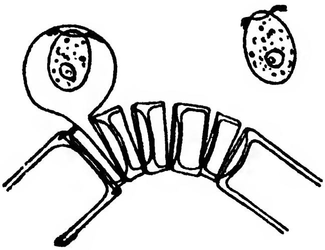


Fig. 513. Escape of androspores of *Oedogonium*

Redrawn after Hirn

egg (Fig. 510). The fertilized egg surrounds itself with a thick wall and becomes an oospore. The oospore is a thick-walled spore and is very resistant to adverse conditions. When the oospore germinates, the protoplast divides to form four zoospores (Fig. 510).

In some species the antheridia occur in ordinary vegetative filaments (Fig. 508); in other species they are found in dwarf male plants (Fig. 512). Dwarf male plants are developed from special spores known as androspores, which are very much like the zoospores but are formed in rows of small cells (Fig. 513). These androspores

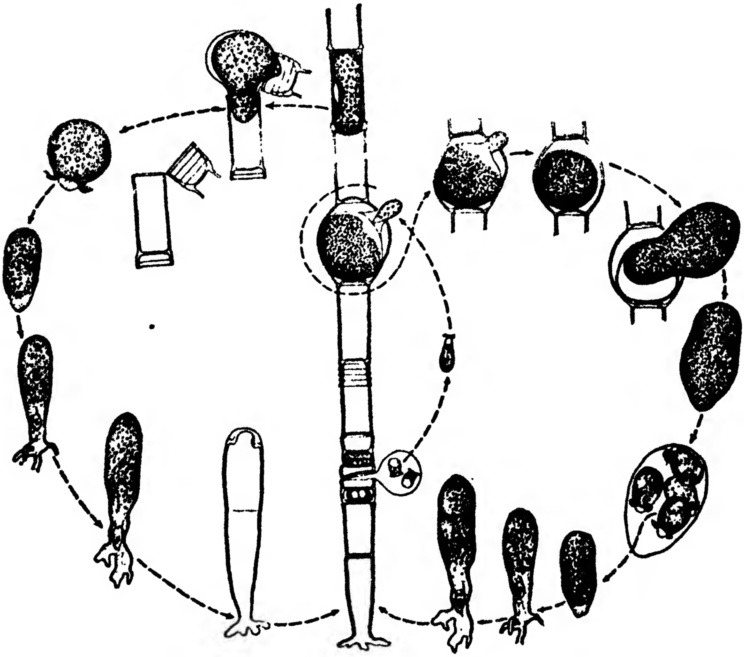


Fig. 514. Life history of *Oedogonium*

To the left, asexual reproduction; to the right, sexual reproduction attach themselves on or near the oogonia, and each grows into a dwarf male which consists of only one or a few cells.

Relationship. *Oedogonium* belongs to the small order *Oedogoniales*, which contains only three closely related genera. Another common genus of this order is *Bulbochaete*, in which the plant consists of a branching filament (Fig. 515). *Bulbochaete* gets its name from the fact that most of the cells bear a long hair with a bulbous base. The *Oedogoniales* seem clearly to be related to other green algae, because they have the green color so characteristic of the group, and also because they store food in the form of starch. The *Oedogoniales* resemble the *Ulotrichales* in that each cell has a single nucleus and a single chloroplast; also in that the cells are arranged in unbranched and branched filaments. However, the method of cell division in the *Oedogoniales* and the presence of a circle of flagella on the motile cells are features which are very different from any found in the *Ulotrichales*; they are so distinctive as to indicate that the *Oedogoniales* represent a different line of evolution from that seen in the *Ulotrichales*, but one which has paralleled the latter in various features. Many botanists believe that the *Oedogoniales* are descended from different unicellular green algae from those which produced the *Volvocales* and *Ulotrichales*. In the *Oedogoniales* there is a highly developed differentiation of sex in that large non-motile eggs are fertilized by small motile spermatozoids. Sexual differentiation in the *Oedogoniales* appears to have developed independently of any similar differentiation of which we know. This is not surprising in view of the fact that differentiation of sexes has been developed independently many times in the plant kingdom.

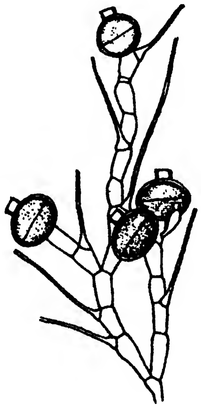


FIG. 515. ***Bulbochaete minuta.*** (× 200)

After Hirn

ORDER *CONJUGALES*, THE CONJUGATING GREEN ALGAE

Spirogyra

General characteristics. A *Spirogyra* plant consists of an unbranched filament composed of similar cells joined end to end (Fig. 516). Each of the cells contains one or more chloroplasts. These chloroplasts have the form of spiral bands. In each chloroplast there is a row of conspicuous rounded pyrenoids. There is a single nucleus, which is in the center of the cell, and which is often plainly visible. Most of the interior of the cell is occupied by a large vacuole. The cytoplasm lines the cell wall, surrounds the nucleus, and extends as fine strands from the cytoplasm around the nucleus to the peripheral cytoplasm. The cells of a *Spirogyra* filament are alike not only in structure but also in function. Each cell performs all the vegetative functions of the plant. Every cell absorbs water, carbon dioxide, and mineral matter; every cell carries on photosynthesis; and every cell has the power of growing and dividing. A filament grows by the division of its cells and the subsequent elongation of the daughter cells. One filament may break into two and thus form two filaments.

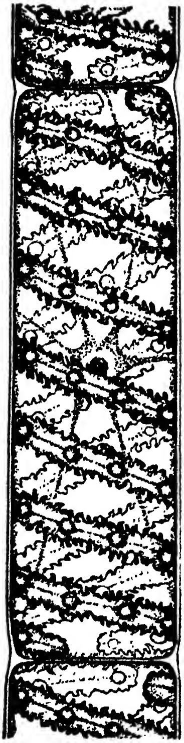


FIG. 516. A cell of *Spirogyra.* (× 425)

Reproduction of *Spirogyra*. Sexual reproduction in *Spirogyra* is by conjugation, which is a union of two similar or nearly similar cells to form a zygospore. In most species this process is initiated by two filaments coming to lie side by side. Projections then grow singly from the cells of each filament to those of the opposite filament (Fig. 517). When the projections from opposite cells come in contact, the walls between them are absorbed so that a tube connects a cell of one filament with a cell of the opposite filament. The protoplasm of one cell then moves through the tube to the opposite cell and fuses with the protoplasm of that cell. When conjugation occurs, it is not confined to one or a few cells, but a large proportion of the cells in the filaments concerned conjugate at approximately the same time. Usually all the cells of a filament behave alike in sexual fusion; for example, if one cell of a filament retains its contents and receives the protoplasm from the opposite cell, all cells in the same filament do likewise. If the filaments having only receiving cells can be considered as indicating a female condition, *Spirogyra* shows what may be regarded as a very slight differentiation of sexes.

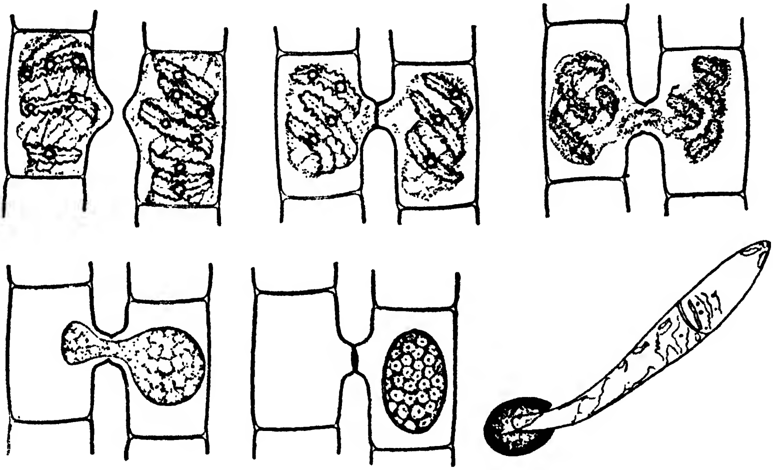


FIG. 517. *Spirogyra*

Successive stages in conjugation and formation of zygospore (× 165) and germination of zygospore

The fusion of the protoplasm of two cells results in the formation of a zygospore, which surrounds itself with a thick wall (Fig. 517). The gametes of *Spirogyra* and of the other *Conjugales* are exceptional among the green algae in that they lack flagella and have amoeboid movements. The entire absence of flagellated cells and the presence of amoeboid gametes are very characteristic features of the *Conjugales*.

The thick walls of the zygospores can withstand adverse conditions. The vegetative cells of *Spirogyra* are killed quickly by drying, while zygospores may be dried for considerable periods and still germinate under favorable conditions. In consequence, the zygospores can be transported from one body of water to another, or when the water in a pool dries up they can survive until they are again surrounded by water. The wall of the zygospore of *Spirogyra*

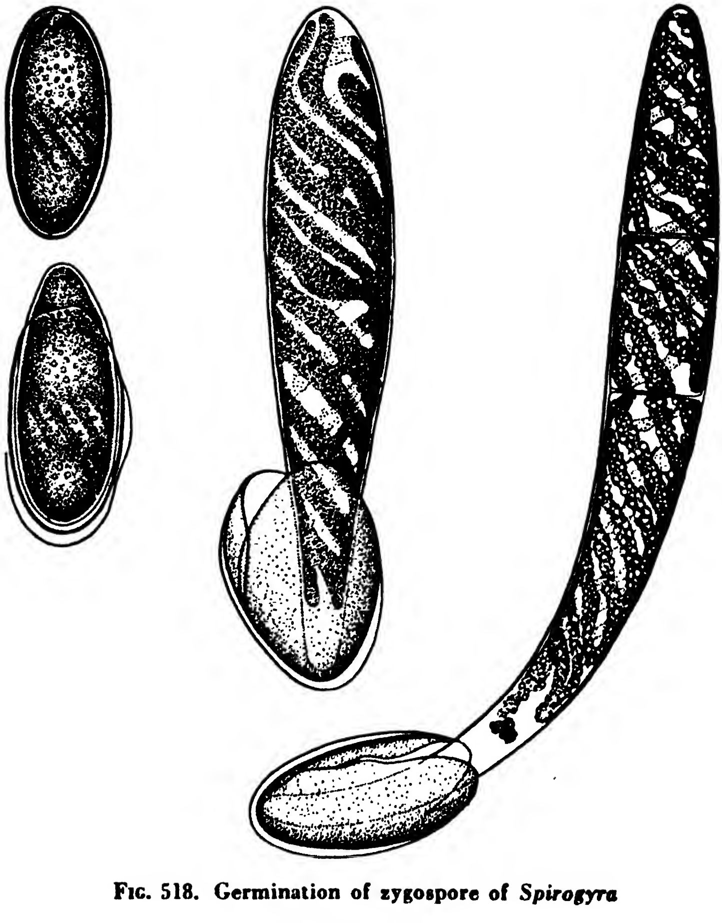


Fig. 518. Germination of zygospore of *Spirogyra*

After Pringsheim

is composed of three layers. When the zygospore germinates the two outer layers are ruptured, and the protoplast of the zygospore, surrounded by the innermost layer of the wall, then grows out to form a filament (Fig. 518).

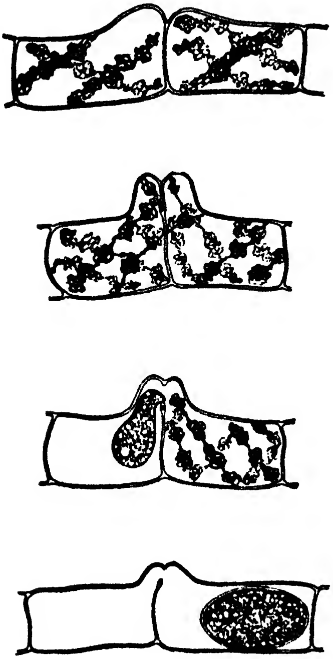


Fig. 519. Stages in the conjugation of *Spirogyra*

Successive stages in conjugation in a species in which conjugation takes place between two neighboring cells of the filament; the lowest figure shows a mature zygospore. (× 200)

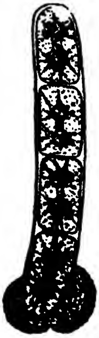


Fig. 520. Young plant of *Zygnema* growing from a spore

After Hallas

Nuclear fusion and division within the zygospore. The two nuclei derived from the two conjugating cells of *Spirogyra* fuse within the zygospore to form the zygospore nucleus. The zygospore nucleus divides to form four nuclei, three of which degenerate, while one persists and becomes a nucleus for the young plant which grows from the zygospore. The cells of the filaments of *Spirogyra* are haploid, while the zygospore nucleus formed by the fusion of the nuclei of the two gametes is diploid. The number of chromosomes is reduced during the division of the zygospore nucleus to form four nuclei. The vegetative filament which grows from the zygospore is therefore haploid.

It is characteristic of both plants and animals that when there is a reduction in the number of chromosomes, there are two reducing divisions so that four nuclei are produced. In many cases all four nuclei are func-

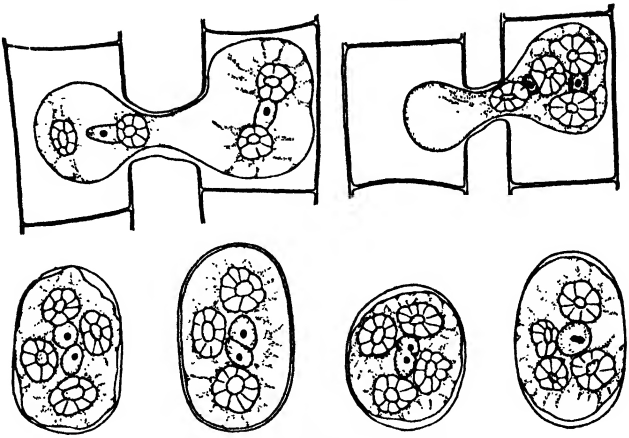


FIG. 521. *Zygnema cruciatum*

Upper line, conjugation; lower line, fusion of nuclei in the zygospore. (× 375). After Kurssanow

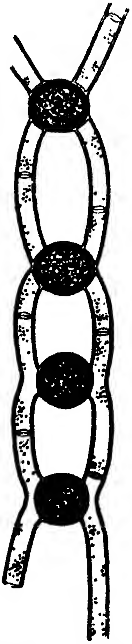


FIG. 522. ***Mougeotia calcarea.*** **(× 300)** **After Wittrock**

tional and each becomes a parent nucleus of a new plant. It is not uncommon, however, for three of the nuclei to degenerate. In seed plants we have seen that the number of chromosomes is reduced in the division of the spore mother cell to form four spores, and that it is usual for three of the spores in an ovule to degenerate.

Lateral conjugation. In some species of *Spirogyra* the zygospore is formed by the conjugation of two adjacent cells in the same filament (Fig. 519). In such cases projections grow from the adjacent ends of the two cells. Where the projections meet, the walls are absorbed so that the two cells are connected by a tube. The protoplast from one cell then enters the other cell and the two protoplasts fuse to form a zygospore.

Relatives of *Spirogyra*. There are a number of filamentous algae which are evidently very closely related to *Spirogyra* and which are placed with *Spirogyra* in the family *Zygnemataceae*.

In the genus *Zygnema*, from which the family gets its name, each cell has two star-shaped chloroplasts (Figs. 520, 521). In some of the *Zygnemataceae* the conjugating gametes are strictly isogametes. This is true in *Mougeotia,* where the contents of the two conjugating cells meet in the conjugating tube and there form the zygote (Fig. 522). Here there is no indication of a differentiation of sexes such as may perhaps be indicated in *Spirogyra.* This condition in *Mougeotia* is also found in some other genera of *Zygnemataceae,* and sometimes in *Zygnema.*

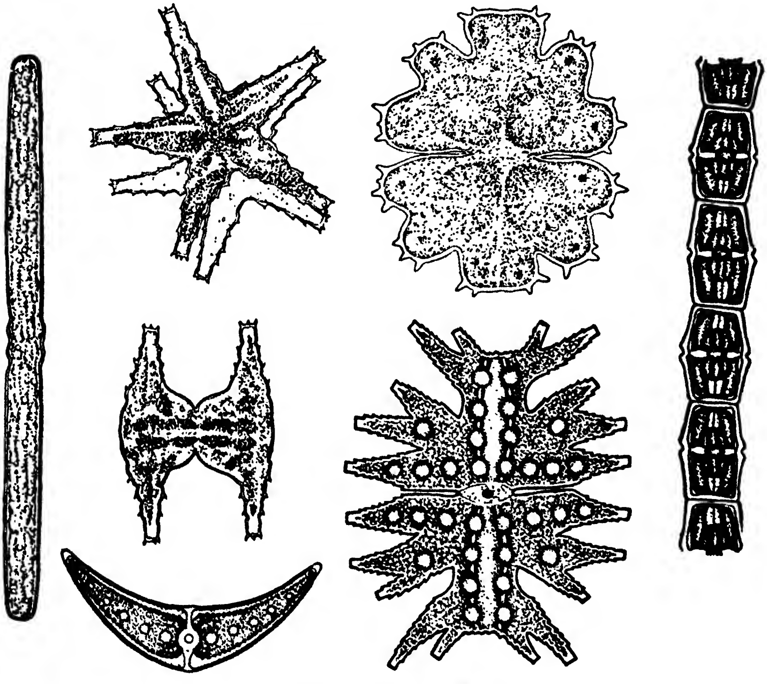


Fig. 523. Forms of desmids

Desmids are either single cells or cells joined together in filaments. They are related to *Spirogyra.* See Fig. 525. (× 220)

Desmids

General characteristics. Related to *Spirogyra* is a group of very beautiful plants known as desmids (Fig. 523). They are mostly unicellular, but in some cases the cells are held together in unbranched filaments. Each cell is composed of two symmetrical halves, which in most cases are sharply marked off from each other by a constriction around the center of the cell. The narrow connecting portion is known as the isthmus. Asexual reproduction takes place by the division of one cell into two across the isthmus; each half then produces a new half similar to itself (Fig. 525). Desmids reproduce sexually by the conjugation of two cells (Figs. 525, 526). In most cases the wall of each cell separates into two parts and the contents escape, migrate toward each other by amoeboid movement, and fuse to form a zygospore which surrounds itself with a thick wall; in other cases the conjugating cells produce conjugating tubes somewhat similar to those of *Spirogyra*. The zygospore nucleus divides to form four nuclei, while the contents of the zygospore divide to form two desmids, each with two nuclei. One of these nuclei degenerates; the other becomes the functional nucleus of the new desmid.

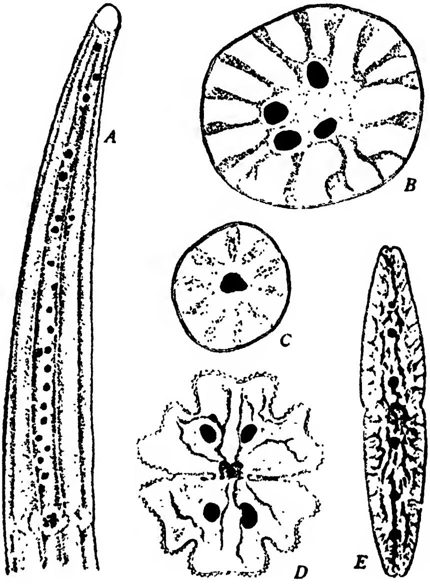


Fig. 524. Chloroplasts of desmids

A, *Closterium attenuatum;* note row of pyrenoids. *B*, transverse section of *Closterium lunula;* note the slender ridges of the chloroplast and the four large pyrenoids. *C*, cross section of *Closterium attenuatum;* note star-shaped chloroplast and single large pyrenoid (compare with *A*). *D*, *Euastrum verrucosum*. *E*, *Tetmemorus granulatus*. (After Carter)

Relationship of *Conjugales.* The desmids are clearly related to *Spirogyra* and other members of the *Zygnemataceae.* Conspicuous in both groups are the occurrence of sexual reproduction by the conjugation of amoeboid gametes and the entire absence of flagellated cells. Not only is there great resemblance between the desmids and the *Zygnemataceae*, but there are connecting forms, often placed among the desmids, which leave no doubt as to there being a close relationship.

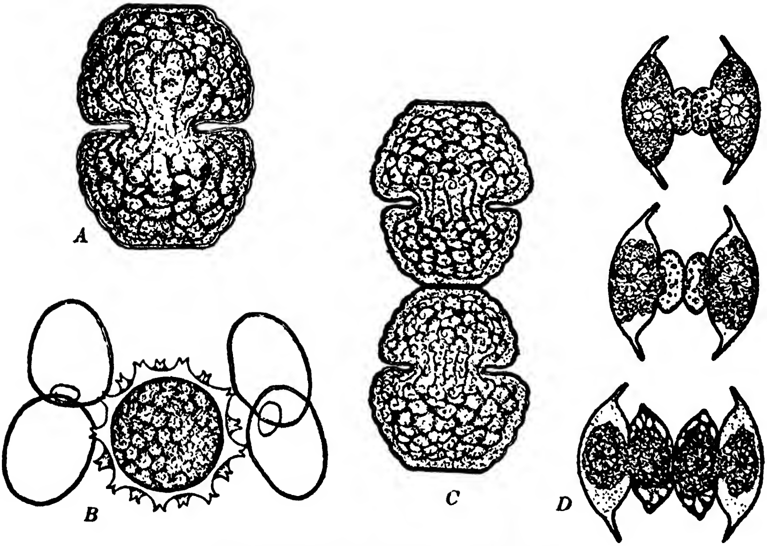


Fig. 525. Reproduction of desmids

A, mature individual of *Cosmarium* (× 1150); *B*, a zygospore (× 700). *C*, a stage in asexual reproduction of *Cosmarium*. *D*, three successive stages in asexual reproduction of *Anthrodesmus* (× 1090)

While the conjugation of amoeboid gametes and the entire absence of flagellated cells make the *Conjugales* a distinctive group, there are sufficient characters, including green color and manufacture of starch, to show that they represent a line of evolution within the green algae. Their conjugation is not unlike the sexual fusion in species of *Chlamydomonas* where this takes place between cells surrounded by cell walls and there is a sort of conjugating tube (Fig. 460). Absence of flagella, due to previous loss, is characteristic of many green algae, especially among the *Chlorococcales.*

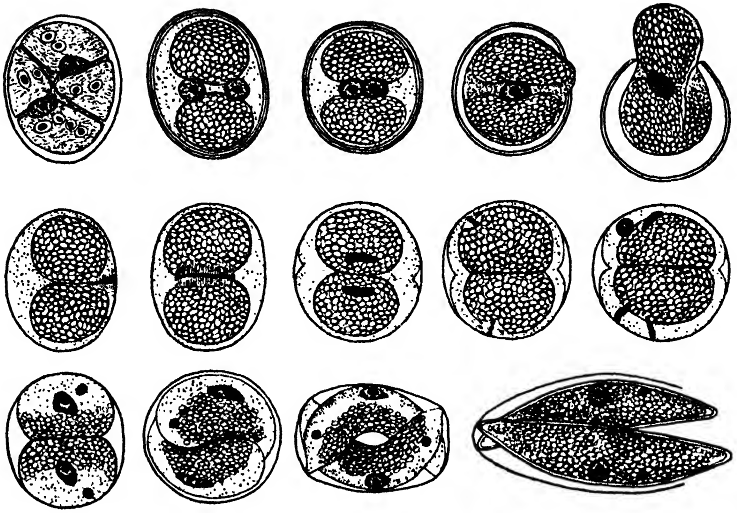


Fig. 526. ***Closterium***

Above, fusion of two nuclei in zygote; middle line, division of zygote nucleus to form four nuclei (the small dark structures in the last figure), and the beginning of the division of the protoplast. Below, formation of two *Closterium* cells; note the presence of one degenerating nucleus in each cell. (After Klebahn)

ORDER *CHLOROCOCCALES*, NON-MOTILE UNICELLULAR AND COLONIAL GREEN ALGAE

Chlorococcum

Systematic position. In the preceding part of this chapter we have considered two lines of evolution in the green algae, the volvocine as exhibited by the *Volvocales* and the tetrasporine as shown by the *Tetrasporales* and the *Ulotrichales*. *Chlorococcum*, which is a primitive member of the *Chlorococcales*, may be thought of as the type of plant which started another line of evolution, the chlorococcine. This line is like the tetrasporine line in that motility is confined to reproductive cells. It is decidedly different, however, as the cells do not divide vegetatively and division of the protoplast occurs only in connection with reproduction. In the more highly developed members of the chlorococcine line the cells may be very large and of very intricate form.

General characteristics. *Chlorococcum* is a round non-motile unicellular alga which when young has a single nucleus and a single large chloroplast with a pyrenoid (Fig. 527). Before reproduction takes place, the cell becomes multinucleate, there is an increase in the number of pyrenoids, and the chloroplast becomes diffuse. *Chlorococcum* reproduces asexually by the division of its protoplast to form zoospores which are biflagellate and have a cup-shaped chloroplast and an eyespot (Figs. 528, 529). They are thus reminiscent of the flagellates and primitive algae from which *Chlorococcum* is believed to have descended. Sexual reproduction is due to the fusion of isogametes (Fig. 530). The formation of the gametes from the protoplast of the mother cell is very similar to the formation of zoospores.

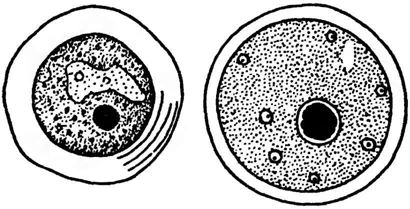


Fig. 527. *Chlorococcum*

Left, exterior view. The irregular light-colored region is the opening in the chloroplast, which otherwise occupies the entire exterior portion of the protoplast. Below the opening the pyrenoid shows as a dark spot. Right, a section of *Chlorococcum* showing seven nuclei and the large pyrenoid. (× 2000). After Bold

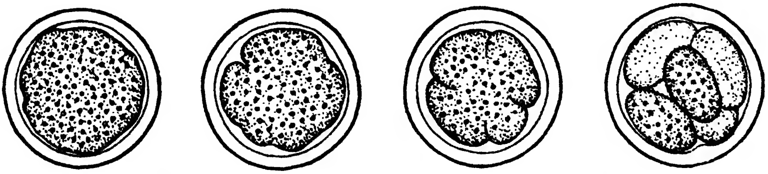


Fig. 528. Division of a protoplast of *Chlorococcum* by cleavage furrows to form zoospores

After Bold

Relationship. *Chlorococcum* may be regarded as having been derived through a modification of *Chlamydomonas*. The *Volvocales*, as we have seen, can be thought of as being derived from the motile stage of *Chlamydomonas*, and the *Ulotrichales* as being due to the development of the palmella stage. In *Chlamydomonas* there is often a phase, before the division of the protoplast to form zoospores or gametes, when the flagella are withdrawn and the

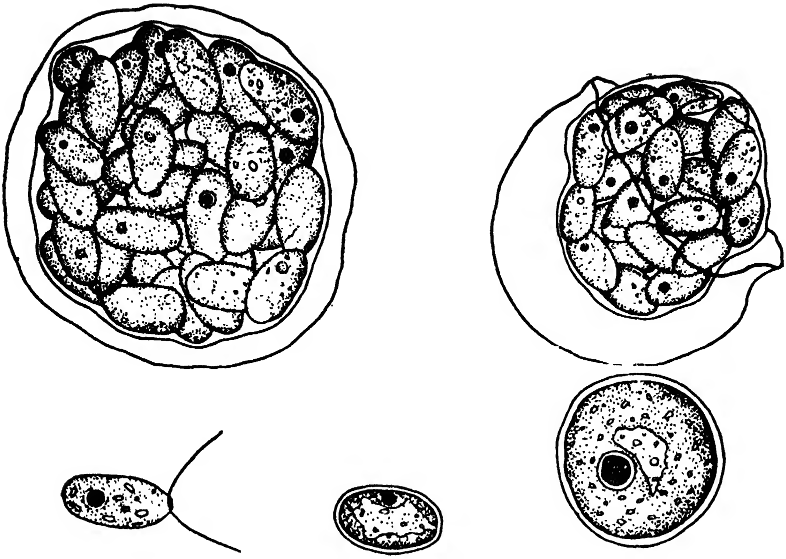


Fig. 529. *Chlorococcum*

Numerous zoospores formed in a large individual, the escape of zoospores, a single zoospore, non-motile cell derived from zoospore, and mature non-motile cell formed by growth from the preceding stage. (× 2000). After Bold

Chlamydomonas cell is for a time non-motile. If this phase were prolonged and the motile and palmella stages suppressed, the result would be such a type as we have in *Chlorococcum.* Here the dominant phase is a non-motile cell. *Chlorococcum* is like most species of *Chlamydomonas* in having one chloroplast and one pyrenoid. Its protoplast divides up in much the same way as that of *Chlamydomonas* to form zoospores and gametes. Its zoospores and gametes are much like those of *Chlamydomonas. Chlorococcum* can, then, be thought of as a *Chlamydomonas* which has lost motility except in reproductive cells.

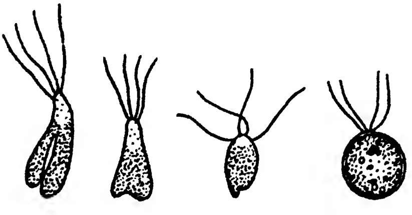


Fig. 530. Fusion of gametes of *Chlorococcum.* (× 1435)

After Bristol

Chlorella

Chlorella is a unicellular alga the cells of which are small and rounded. Each has a single chloroplast, which is usually cup-shaped (Fig. 531). The only method of reproduction is by the division of the protoplast to form two, four, eight, or sixteen parts, each of which becomes surrounded by a cell wall to form a non-motile cell (Fig. 531). These are like the parent cell except for size. They are liberated by the disintegration of the wall of the mother cell and grow to mature size. We have noted that in the most primitive of the green algae, and in the flagellates from which they are descended, the motile phase is dominant. *Chlorococcum* is a unicellular form in which this condition is reversed, the non-motile stage being dominant. In *Chlorella* the reduction of the motile phase has reached the extreme, as in this unicellular alga there are no motile cells.

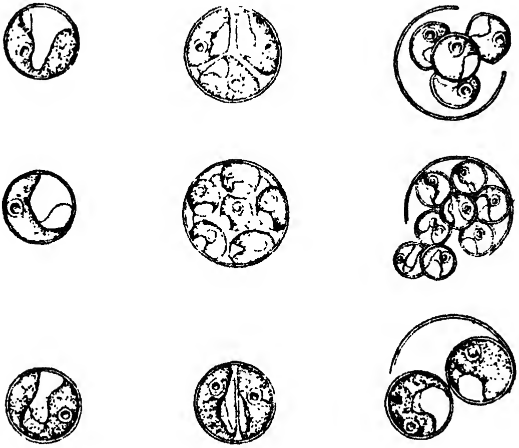


FIG. 531. *Chlorella vulgaris*

Upper line, formation of four daughter cells from mother cell; second line, formation of eight daughter cells; third line, formation of two daughter cells. (After Grintzesco)

Non-Motile Colonial Algae

In the early part of this chapter we saw that the primitive unicellular motile green algae have given rise to a variety of colonial forms. In a similar way non-motile unicellular algae, of which *Chlorococcum* and *Chlorella* may be taken as examples, gave rise to non-motile colonial forms. In some cases reproduction is through the formation of motile cells as in *Chlorococcum*, while in others motile reproductive cells are entirely lacking just as they are in *Chlorella*.

***Pediastrum*.** The individual plants of *Pediastrum* are microscopic flat plate-shaped colonies of cells (Fig. 532). They are common, widely distributed, and very beautiful fresh-water algae. In young colonies each cell has a single nucleus, but in older colonies there may be as many as eight nuclei. This multinucleate condition is brought about by a division of the nucleus without cell division. The presence of nuclear division without cell division is, as previously noted, characteristic of the chlorococcine line of evolution. Any cell of a colony of *Pediastrum* is capable of reproducing the colony asexually through the production of zoospores. After the formation of zoospores a slit appears in the outer layer of the cell wall. The zoospores escape through this slit, but are still surrounded by a vesicle formed from the inner layer of the cell wall (Fig. 533). The cells of this colony grow and take on the form of mature cells. *Pediastrum* may reproduce sexually by the formation of biflagellate gametes (Fig. 533).

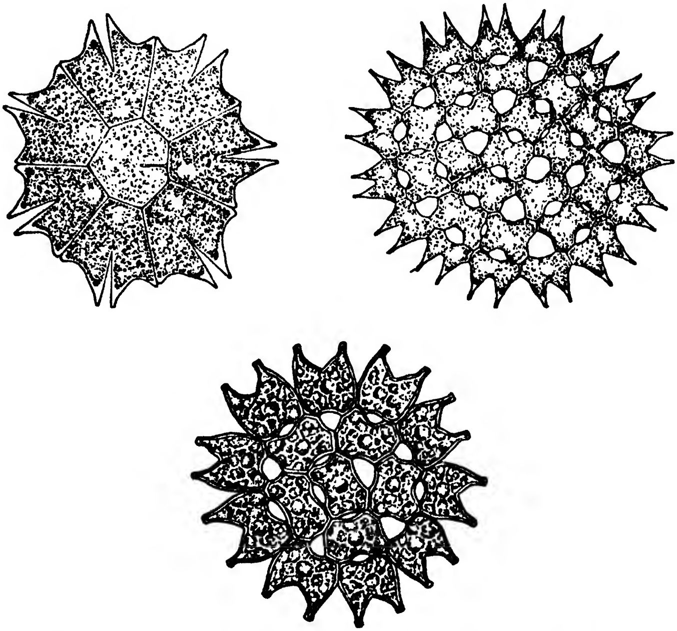


Fig. 532. Three forms of *Pediastrum*, a colonial green alga. (× 210)

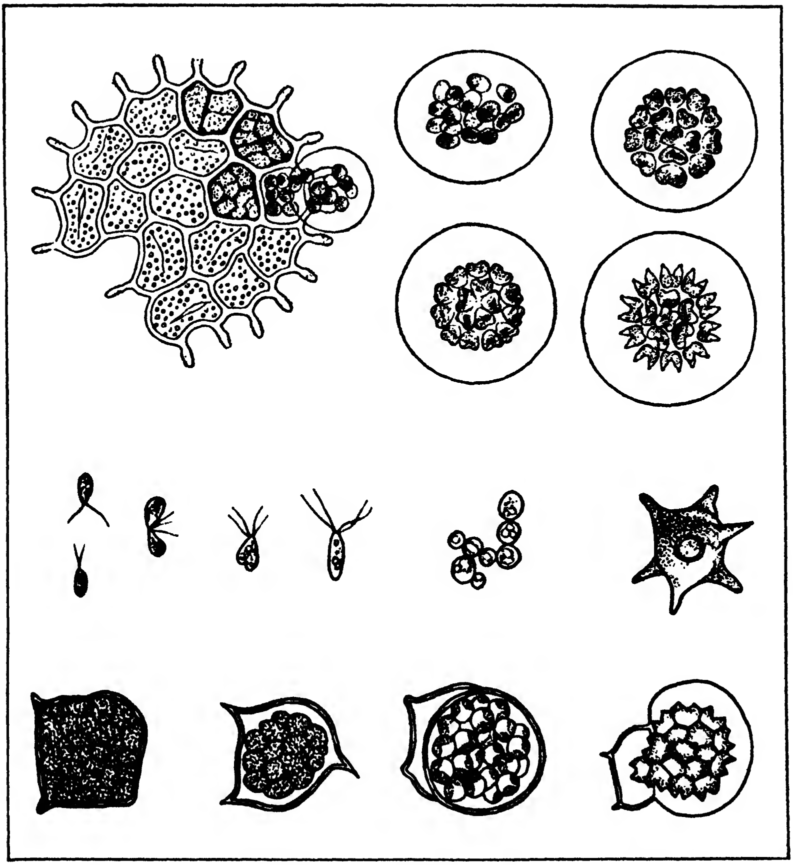


FIG. 533. *Pediastrum*

Upper left, formation of zoospores and escape of zoospores in vesicle; upper right, zoospores still surrounded by vesicle forming a colony; center, gametes, fusion of gametes to form zygote, and large angular spore formed from zygote; lower line, division of contents of angular spore to form zoospores and escape of zoospores in vesicle to form colony. (After Braun and Askenasy)

Hydrodictyon. The water net, *Hydrodictyon*, has cylindrical cells which are united to form a conspicuous elongated sac-shaped net (Figs. 534, 535). The water net is widely distributed and fairly common. The nets may be as much as 30 cm. in length, but are usually smaller. When young, each cell contains a single nucleus; but as they grow the number of nuclei increases, and in a mature cell there are numerous nuclei. Just as *Volvox* may be regarded as the culmination of motile colonies, so *Hydrodictyon* may be thought of as the culmination of non-motile colonies which reproduce by motile cells. Each cell of the net of *Hydrodictyon* is capable of asexual reproduction through the formation of a daughter net

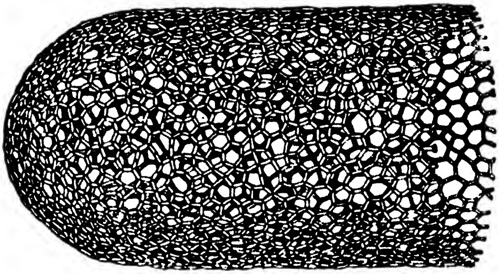


FIG. 534. Portion of net of *Hydrodictyon reticulatum*

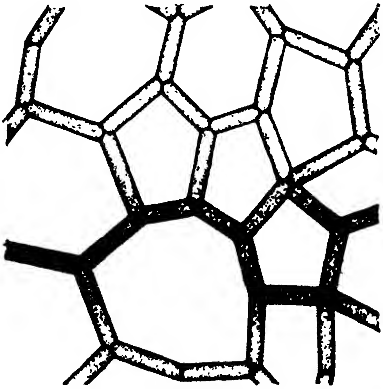


FIG. 535. Small portion of net of *Hydrodictyon reticulatum*, showing shape and arrangement of cells

within itself. The protoplast of the daughter cell divides up to form very numerous zoospores. These swarm about for a time, after which they become arranged around the periphery of the mother cell, and by growth, without further cell division, form a new net. As a new net is formed within a parent cell, it naturally takes the shape of that cell. A net is liberated by the disintegration of the wall of the parent cell, after which the cells of the new net continue to grow.

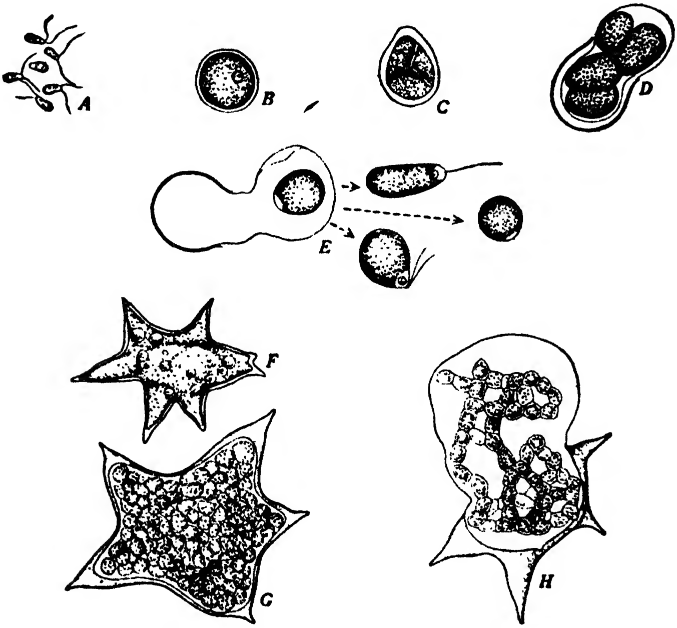


FIG. 536. Sexual reproduction in *Hydrodictyon*

A, gametes; *B*, mature zygote; *C*, zygote dividing to form four zoospores; *D*, zoospores escaping in vesicle; *E*, three of the four zoospores have escaped; *F*, thick-walled angular spore formed from zoospore; *G*, division of contents of angular spores to form zoospores; *H*, young net formed from zoospore escaping in a vesicle

Sexual reproduction is due to the fusion of biflagellate gametes (Fig. 536). These are formed in the same manner as zoospores, but escape through an opening in the wall of the mother cell. Two gametes fuse to form a zygote. The protoplast of the zygote divides up to form four zoospores (Fig. 536), and meiosis, or the reduction in the number of chromosomes, occurs in the nuclear divisions which lead to their formation. After swimming for a time, the zoospores form curiously shaped, thick-walled, angular spores. The angular spore increases greatly in size, and its contents divide up to form a considerable number of zoospores. These, surrounded by a vesicle, escape from the spore in much the same way as the zoospores of *Pediastrum* escape from their mother cell. Within the vesicle the zoospores form a small irregular net (Fig. 536).

Scenedesmus. The colony of *Scenedesmus* consists of a single row of cells or of two rows (Fig. 537). *Scenedesmus* is very common and widely distributed in fresh waters. The only method of reproduction known is by the division of the protoplast of a cell to form a new colony (Fig. 538). Each cell of the new colony surrounds itself with a cell wall, and the new colony is set free by the disintegration of the wall of the mother cell. In the absence of both sexual reproduction and motile reproductive cells *Scenedesmus* resembles *Chlorella.*

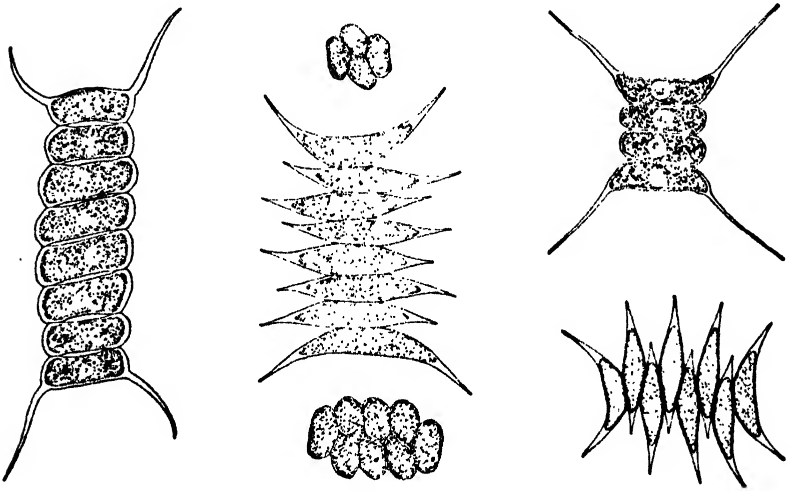


FIG. 537. Various forms of *Scenedesmus.* (× 500)

Coelastrum. This is a very common, widely distributed, and beautiful microscopic alga. The colony consists of a single layer of cells arranged in the form of a hollow sphere (Fig. 539). Reproduction is very similar to that of *Scenedesmus*, and consists in the formation of a daughter colony within a cell of the mother colony, the daughter colony being set free by the disintegration of the wall of the mother cell (Fig. 540). In the absence of both sexual reproduction and motile reproductive cells *Coelastrum* re-

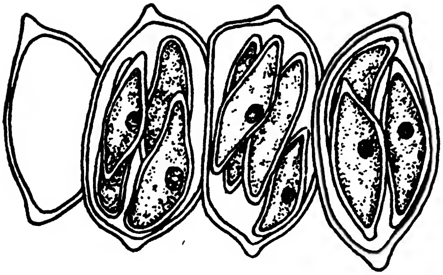


Fig. 538. *Scenedesmus acutus*

Formation of daughter colonies in cells of mother colony. (× 2200). After Senn

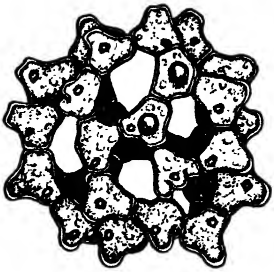


Fig. 539. *Coelastrum proboscideum*. (× 450)

After Senn

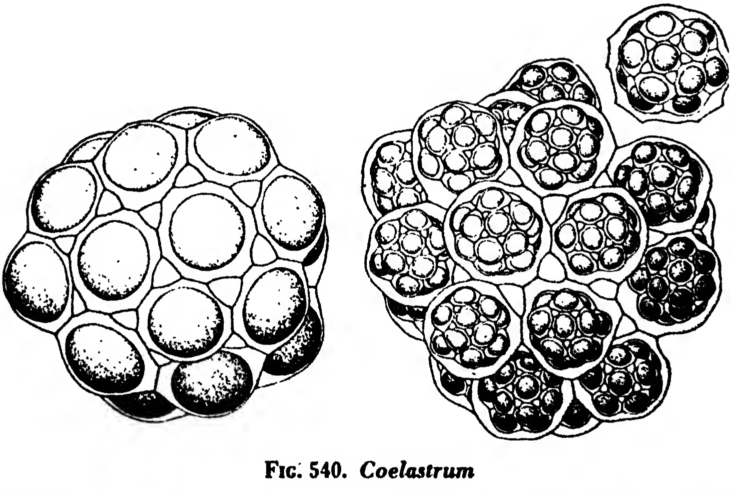


Fig. 540. *Coelastrum*

Left, a colony; right, a colony the individual cells of which have divided to form daughter colonies, one of which is separating. (× 900)

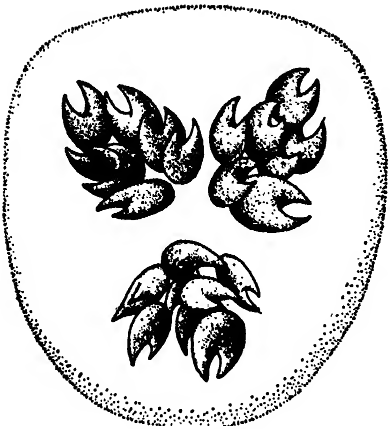


FIG. 541. *Kirchneriella*, a colony in which the individuals are held together loosely in a gelatinous matrix

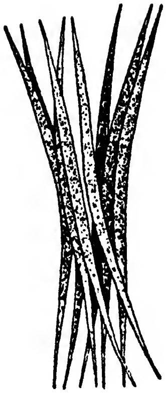


FIG. 542. *Ankistrodesmus*, a loose aggregate of cells

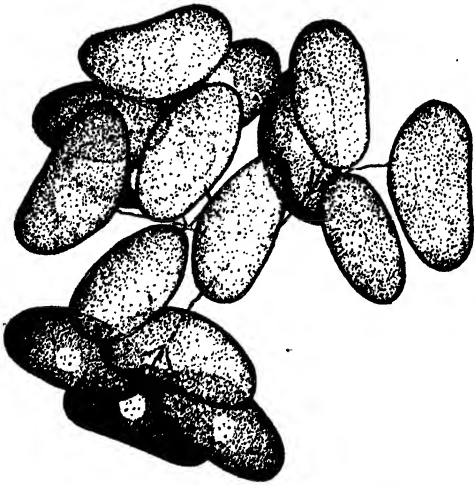


FIG. 543. *Dimorphococcus*, a colony in which the cells are held together in groups of four by the remains of the wall of the mother cell. The groups of four are likewise held together by remains of cell walls. (× 1225)

sembles *Scenedesmus* and *Chlorella*. It is, however, difficult to be sure as to whether it is a highly developed colony descended from an ancestry lacking motile cells, or whether it may not have been derived, through loss of motility, from a relative of some such colonial form as *Hydrodictyon*.

ORDER *SIPHONALES*, COENOCYTIC GREEN ALGAE

Vaucheria

General characteristics. The filamentous alga *Vaucheria* is the common fresh-water representative of the order *Siphonales*. The order is characterized by the fact that the vegetative portion of the plant consists of branching filaments with many nuclei but no cross walls. Cross walls normally occur only in connection with reproductive organs (Fig. 544).

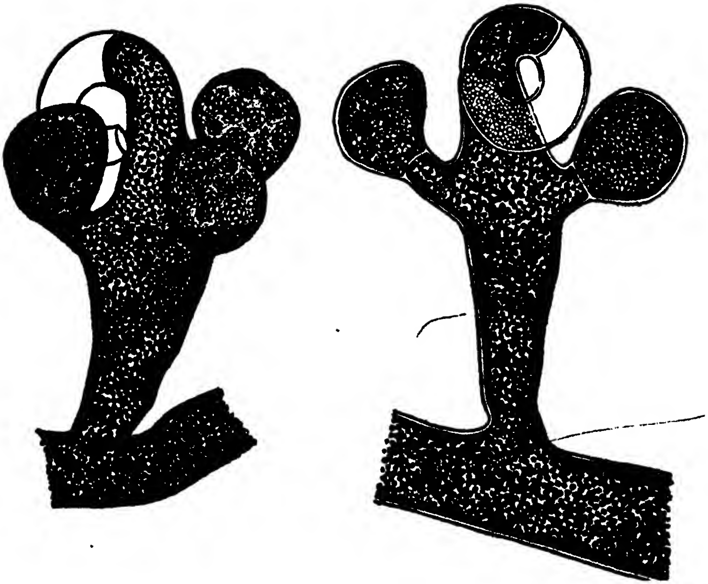


FIG. 544. Branches of *Vaucheria*

Left, branch with three oogonia and empty antheridium; right, branch with two oogonia and empty antheridium. (× 185)

Vaucheria forms conspicuous feity green mats. The plant consists of sparingly branched filaments, in the vegetative portion of

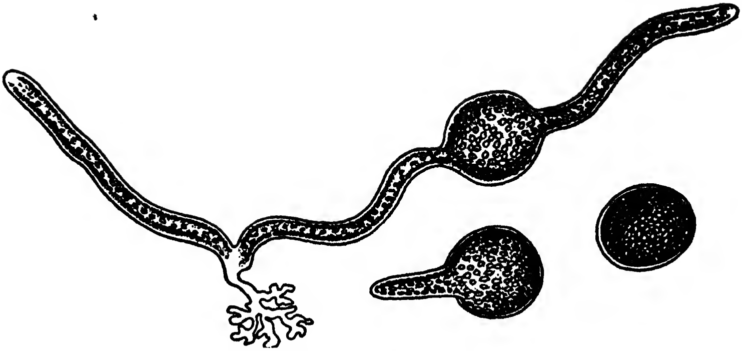


Fig. 545. Germination of zoospore of *Vaucheria*

Redrawn after Sachs from Oltmanns

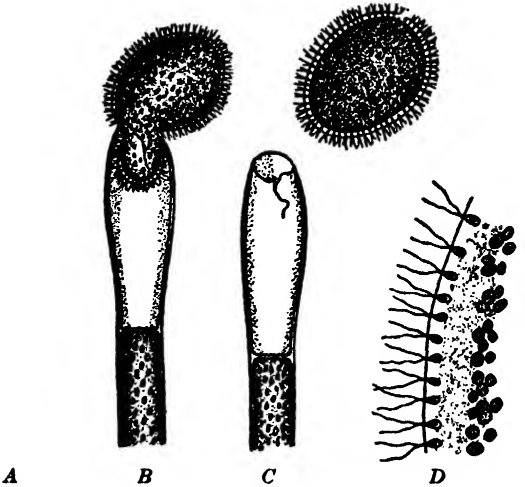


Fig. 546. *Vaucheria*

A–C, formation and escape of zoospore; *D*, section of a portion of zoospore, showing two flagella opposite each nucleus. (*A–C* redrawn after Goetz from Oltmanns; *D* redrawn after Strasburger from Oltmanns) which there are no cross walls. The cell wall is lined with protoplasm, while a vacuole extends through the center of the filament. Numerous nuclei and chloroplasts occur in the protoplasm. The plant is attached to the substratum by colorless branching filaments (Fig. 545). Plants in which there are many nuclei and in which the protoplast is continuous owing to the absence of cross walls are called coenocytes.

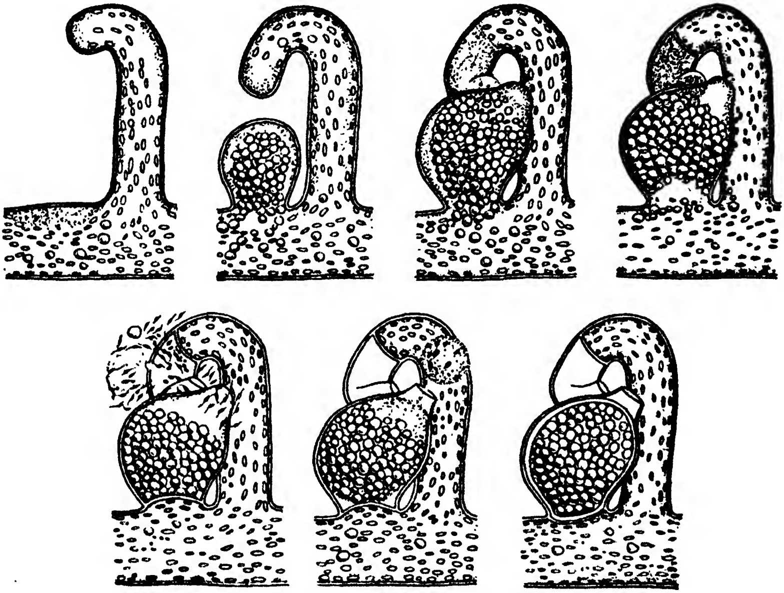


FIG. 547. *Vaucheria sessilis*

Upper line shows development of antheridium and oogonium. Lower left, antheridium is mature and sperm has been discharged, oogonium still closed; center, oogonium has opened and discharged a small amount of protoplasm and is ready for fertilization; right, oogonium has been fertilized and contains an oospore. (× 244). After Couch

Asexual reproduction. The most frequent method of asexual reproduction in *Vaucheria* is by the formation of large compound zoospores. The zoospores are produced singly in zoosporangia, which are formed at the ends of filaments. In the formation of a zoosporangium the end of a filament enlarges and is cut off from the remainder by a cross wall. The contents are then transformed into a large oval zoospore (Fig. 546). This contains many nuclei and has numerous flagella, which occur in pairs, each pair being opposite a nucleus. This type of zoospore is a very peculiar one on account of the fact that it contains many nuclei and has flagella distributed over its entire surface. Many of the relatives of *Vaucheria* have an ordinary type of zoospore. These are produced in large numbers in a zoosporangium, and each has a single nucleus and two flagella. Since in the zoospore of *Vaucheria* a pair of flagella is opposite each nucleus, this zoospore has been interpreted as a compound one which has resulted from the failure of the protoplast to divide and produce uninucleate zoospores as is the case in relatives of *Vaucheria.*

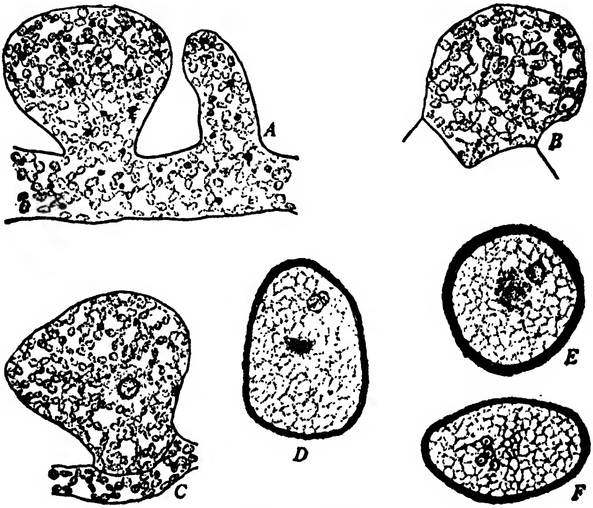


Fig. 548. *Vaucheria*

A, section of young stages of oogonium and antheridium; note the numerous nuclei. *B*, oogonium is cut off by a cell wall and all except one of the nuclei are degenerating while this is enlarging. *C*, only one nucleus remains in the oogonium. *D*, section of oospore showing fusion of male and female nuclei. *E*, a late stage showing oospore nucleus formed by fusion of male and female nuclei. *F*, still later stage; oospore nucleus has divided to form four nuclei. (× 240). After Williams

The zoospore of *Vaucheria* escapes through an opening produced by the softening of the wall at the tip of the zoosporangium.

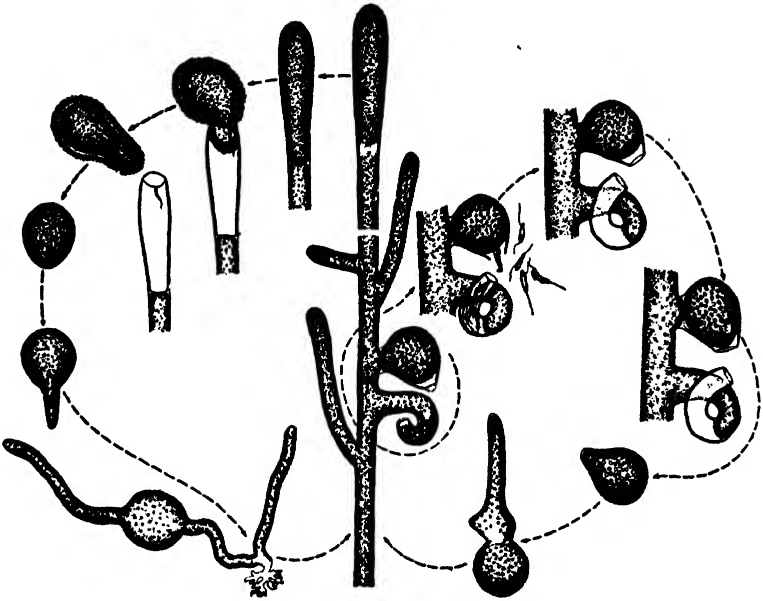


FIG. 549. Diagram of life history of *Vaucheria*

Center, mature plant; left, asexual reproduction; right, sexual reproduction

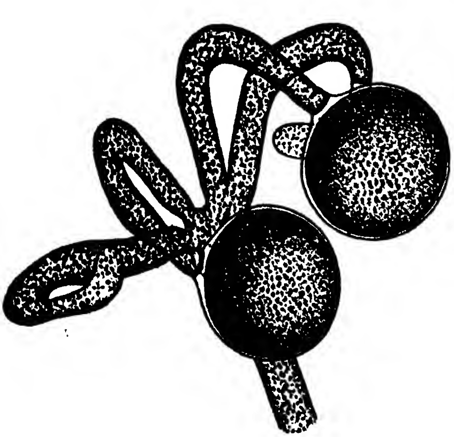


FIG. 550. ***Dichotomosiphon tuberòsus*, showing two oogonia and two antheridia**

Dichotomosiphon tuberosus **is a close relative of** ***Vaucheria*****. (× 75). After Ernst**

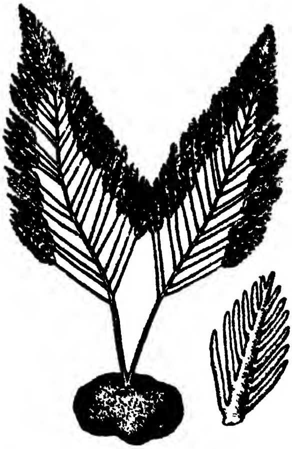


FIG. 551. ***Bryopsis*****, one of the** ***Siphonales*****. (× ½)**

Lower right, portion of a plant enlarged

After swimming about for a while the zoospore comes to rest, develops a cellulose wall, and grows into a new plant (Fig. 545). In this process the zoospore produces two tubular filaments, one of which develops a holdfast by which the plant becomes attached to the substratum.

Sexual reproduction. *Vaucheria* reproduces sexually by means of eggs and spermatozoids. The eggs occur singly in oogonia, while the spermatozoids are produced in considerable numbers in antheridia (Fig. 547). The oogonia and antheridia are either developed directly from the vegetative filament (Fig. 547) or occur on short branches (Fig. 544). The oogonium is a large round structure, usually with a projection or beak, and is cut off from the main filament by a wall. It contains a single egg, which when mature has only one nucleus (Fig. 548). Young oogonia are multinucleate, but there is a disintegration of all nuclei except the one which is to function as the egg nucleus. The antheridium is a small tubular branch which is usually curved at the time of maturity. The antheridium is cut off from the vegetative filament by a cross wall. When the egg is mature, the oogonium opens at the beak. The mature antheridia also open and in this way allow the spermatozoids to escape. These swim around, and some reach an oogonium, where one of them fuses with the egg. The fertilized egg surrounds itself with a thick wall and becomes a resting oospore. After a period of rest it develops directly into a new plant.

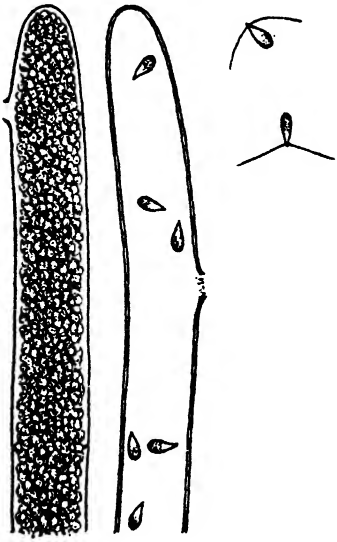


FIG. 552. *Bryopsis*
Gametangia and gametes. (× 330). After Thuret

Relatives of *Vaucheria*. Most of the relatives of *Vaucheria* are salt-water forms in which sexual reproduction is by the fusion of large and small gametes (heterogametes). In sexual differentiation such forms are

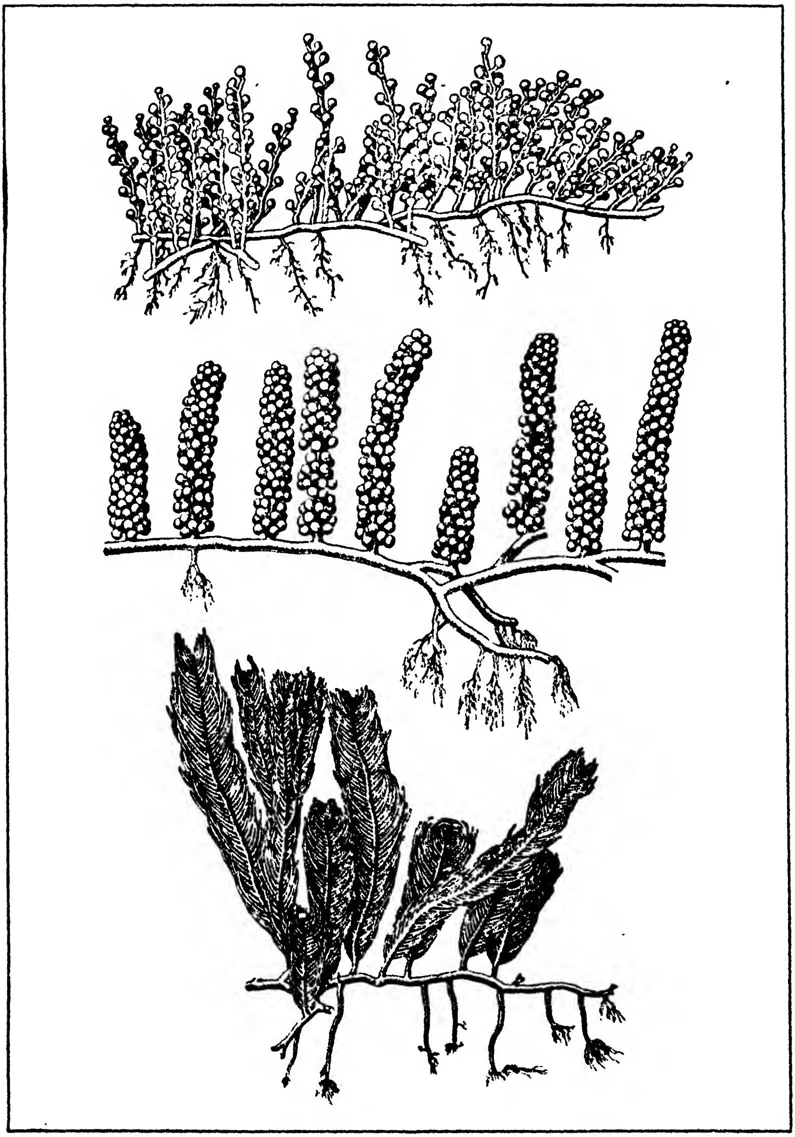


Fig. 553. Three species of *Caulerpa*

Caulerpa is one of the *Siphonales*. The plant is a single coenocyte without cross walls. (Upper figure × $\frac{3}{8}$; two lower figures × $\frac{3}{4}$)

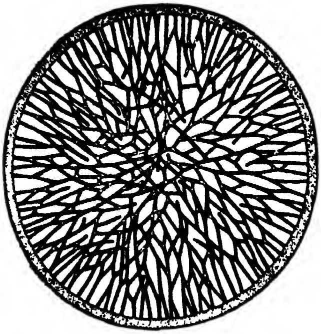


Fig. 554. Cross section of a branch of *Caulerpa* showing cross supports which protect the plant from undue swelling or bursting as a result of osmotic pressure

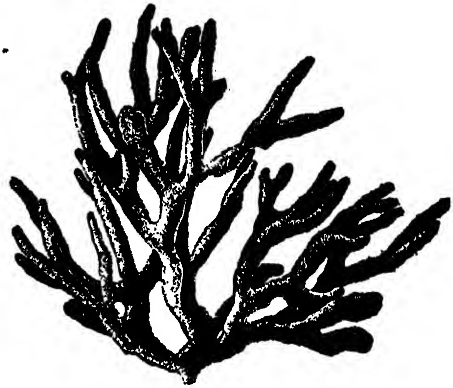


Fig. 555. *Codium*, a siphonaceous alga

The plant is composed of interlacing hyphae. See Fig. 556

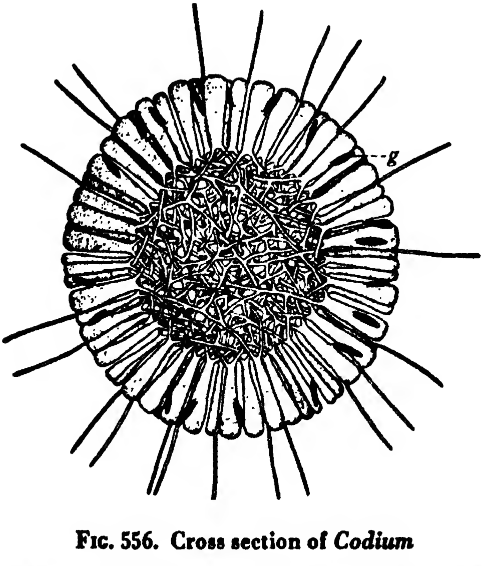


Fig. 556. Cross section of *Codium*

The plant is made up of interlacing filaments without cross walls. Note the gametangia *g* which project from the sides of the large club-shaped portions of the filaments which form a sort of cortex less advanced than *Vaucheria*. However, many of them have a much more complicated vegetative structure than *Vaucheria*.

In *Bryopsis* (Figs. 551, 552) the lower branches are modified as organs of attachment, while the upper ones form graceful featherlike fronds. As in *Vaucheria*, the plant is a coenocyte consisting of branched tubes in which are numerous nuclei but no cross walls.

Caulerpa is a beautiful and interesting genus which is common in tropical waters (Fig. 553). This plant simulates the vegetative differentiation seen in higher plants. The thallus has creeping rhizomelike branches. From the upper surface of such a branch there arise branches which roughly resemble foliage shoots, while from the lower surface grow colorless rootlike branches. *Caulerpa*, like the *Siphonales* in general, lacks cross walls. The form is maintained by turgor, while the branches are protected from undue swelling or bursting by a network of cross supports (Fig. 554). This genus is of interest not only on account of the large size and high degree of differentiation of a single coenocyte, but also because no reproduction by special bodies, either sexual or asexual, is known. Reproduction is due to the separation of proliferous shoots.

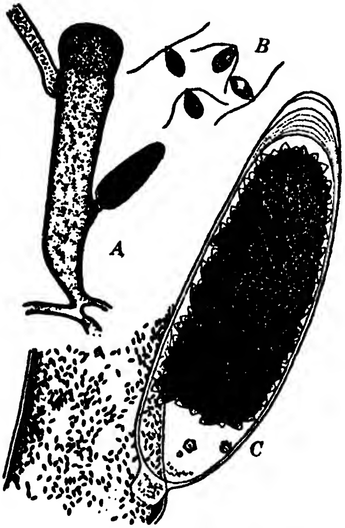


FIG. 557. *Codium tomentosum*

A, club-shaped branch with gametangium; *B*, gamete; *C*, enlarged view of gametangium with gametes. (× 165). After Thuret

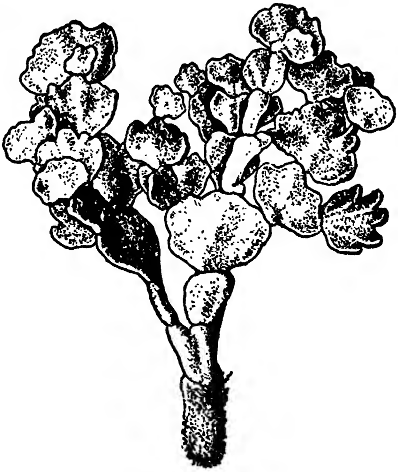


FIG. 558. *Halimeda opuntia*, a calcareous green alga

In *Codium* the branches of the coenocytic plant body are interlaced in such a way as to produce a large plant with definite form (Figs. 555–557).

These plants have a spongy feel, which is connected with the fact that they are formed of interlacing branches. Various other genera in which the plant is composed of interlacing branches have characteristic shapes.

Relationship of *Siphonales*. *Vaucheria* and the other *Siphonales* appear to be descended from the *Chlorococcales*. We have seen that among the *Chlorococcales* there is an absence of vegetative cell division and a tendency for the development of multinucleate cells. There are some forms which are so much on the border line between the *Chlorococcales* and the *Siphonales* that it is difficult to decide in which group to place them (Fig. 560), and authorities disagree.

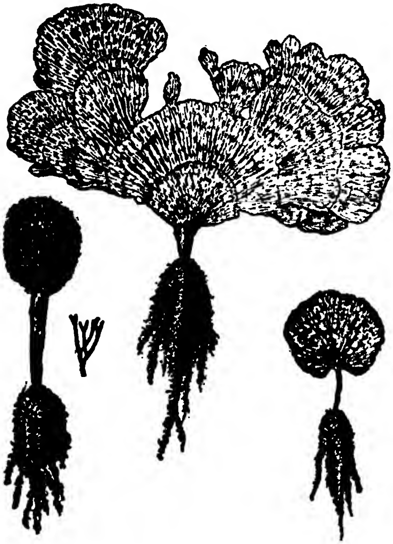


Fig. 559. Three of the *Siphonales*

Left, *Penicillus capitatus*. The small figure shows the details of filaments. Center, *Udotea flabellum*; right, *Udotea orientalis*. These algae are coenocytes. *Udotea* is formed of interlacing filaments. Habit sketches. (× ⅓)

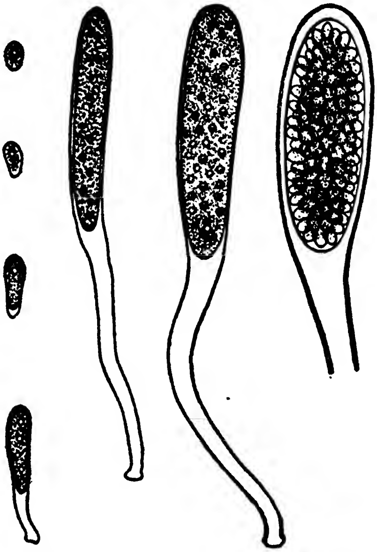


Fig. 560. ***Codiolum gregarium*, an alga which is on the border line between the *Chlorococcales* and *Siphonales*. (× 65)**

After Braun

Protosiphon (Fig. 561) is a border-line genus which illustrates the way in which the *Siphonales* may have been derived from the *Chlorococcales*. *Protosiphon* is a small coenocytic alga. It has a rounded bladderlike aerial portion which tapers into an elongated colorless underground portion. *Protosiphon* is like *Chlorococcum* in that the protoplasm may divide to form biflagellate zoospores (Fig. 561) or may divide in a similar manner to produce biflagellate isogametes. The gametes fuse in pairs to form zygotes, which may germinate directly into vegetative coenocytes (Fig. 562). *Protosiphon* could be thought of as a *Chlorococcum* which has developed a colorless outgrowth suitable for absorbing materials from the

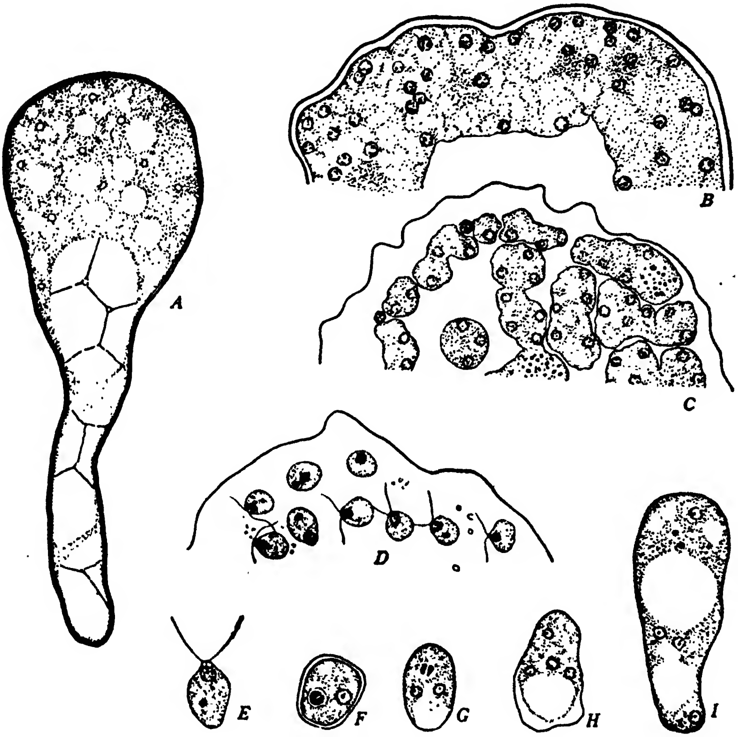


FIG. 561. *Protosiphon*

A, longitudinal section of almost mature thallus. *B*, section of upper portion of thallus showing the numerous nuclei. *C*, section of upper portion of thallus showing protoplasm dividing up by cleavage furrows; when the process is completed each segment will contain a single nucleus and will form a zoospore. *D*, section of upper portion of thallus showing zoospores. *E*, zoospore. *F–I*, stages in germination of zoospore; note that the plant soon becomes multinucleate. (After Bold)

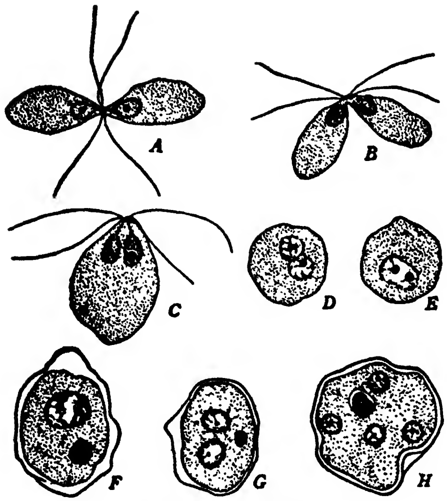


Fig. 562. *Protosiphon*

Fusion of gametes and germination of zygote. (After Bold)

substratum. Also, it could be thought of as having the characteristics of a very simple ancestor of the *Siphonales*. In the *Siphonales*, as in various other lines of green algae, we see the development of the differentiation of sex. The *Siphonales* must have been descended from some form in which, as in *Protosiphon*, sexual reproduction was due to the fusion of isogametes. In the majority of the *Siphonales* there is a fusion of heterogametes, while in *Vaucheria* we have oogamy, in which very large non-motile eggs are fertilized by minute motile spermatozoids.

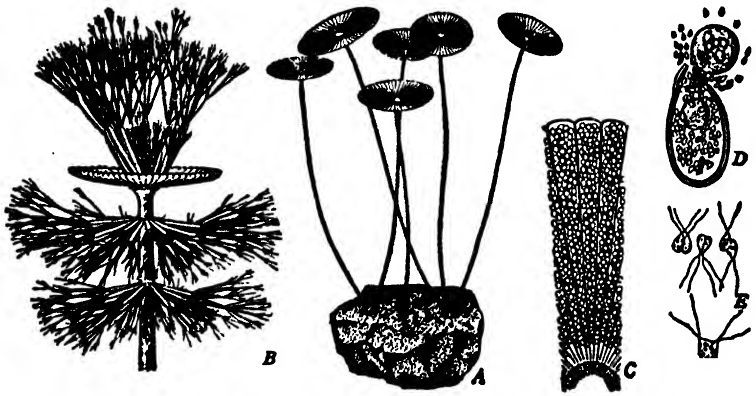


Fig. 563. *Acetabularia mediterranea*, one of the *Siphonocladiales*

A, mature plant with sporangia arranged in an umbrellalike manner (× 1); *B*, young plant showing evanescent branches and early stage in the formation of the umbrellalike top (× 5); *C*, portion of umbrellalike top showing sporangia with "aplanospores"; *D*, an "aplanospore" liberating gametes; *E*, fusion of gametes. (*D*, *E*, after De Bary and Strasburger)

ORDER *SIPHONOCLADIALES*

General characteristics. The order *Siphonocladiales* is composed of marine species and is closely related to the *Siphonales*. In most cases the plant is composed of a comparatively small number of large multinucleate cells. These are often arranged in a very definite and complicated manner to form interesting and beautiful plants (Figs. 563, 564). The *Siphonocladiales* are generally regarded as being derived from the *Siphonales* by the development of cross walls. In the *Siphonales* reproductive structures are cut off by cross walls. The simplest of the *Siphonocladiales* are very similar to the *Siphonales*, and from these simple forms there can be traced a tendency toward an increase in septation and the complexity of the plant

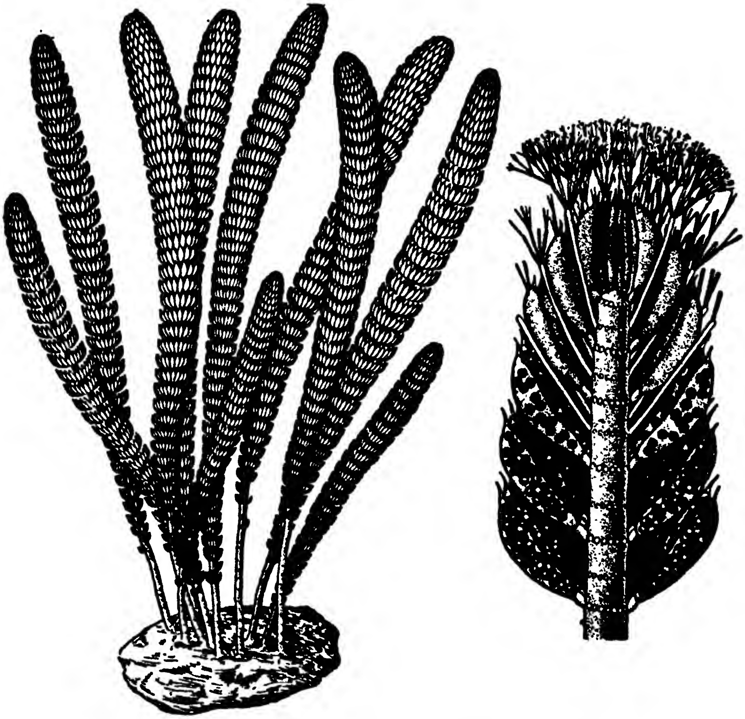


FIG. 564. *Halicoryne*, one of the *Siphonocladiales*

Left, habit (× 1); right, portion of tip showing development of sporangia. Notice that near the tip evanescent sterile branches alternate with the young sporangia. In this drawing the branches and sporangia in front have been removed. (× 6) body. According to another theory the *Siphonocladiales* have been derived from the *Ulotrichales* through some such ancestry as *Cladophora* (Figs. 505, 506).

Acetabularia. This is a branching alga, the development of which culminates in the production of a beautiful umbrella-like structure (Fig. 563). The umbrella top is composed of a whorl of elongated cells which are sometimes called sporangia. Within each of these there develop a large number of ellipsoidal structures often called "aplanospores." The "aplanospores" are set free, and after a period of rest a large number of biflagellate isogametes (Fig. 563) develop within each "aplanospore." These fuse in pairs to form zygospores, which, after a period of rest, germinate directly into new plants.

In *Halicoryne* the fertile branches or "sporangia" are borne in whorls one above the other (Fig. 564). Near the tip there are whorls of evanescent sterile branches alternating with the fertile branches.

SUMMARY OF GREEN ALGAE

The great groups. Within the green algae there are three great aggregations of plants (Fig. 565). The first consists of motile forms, both unicellular and colonial. Among the simplest of such forms is the unicellular *Chlamydomonas*, where sexual reproduction is usually isogamous. The most complex are found in the genus *Volvox*, where the colony may consist of thousands of cells, where there is a sharp distinction between vegetative and reproductive cells, and where sexual reproduction is oogamous, due to the fertilization of a large non-motile egg by a small motile spermatozoid. The whole aggregation of motile forms belong in the order *Volvocales*, the volvocine green algae.

Another large aggregation consists of the filamentous and expanded forms found in the order *Ulotrichales*. In these forms vegetative divisions are prominent, and result in a considerable development of vegetative cells and usually in a multicellular body. Here again we find great diversity in the structure of the various plants. Also, there are various grades in the differentiation of sexuality. Sexuality varies from isogamy such as is found in *Ulothrix* to the highly developed oogamy seen in *Coleochaete*. The *Oedogoniales* and *Conjugales* parallel the *Ulotrichales* by having an extensive development of vegetative divisions, while parallel development is also shown by the filamentous condition in the

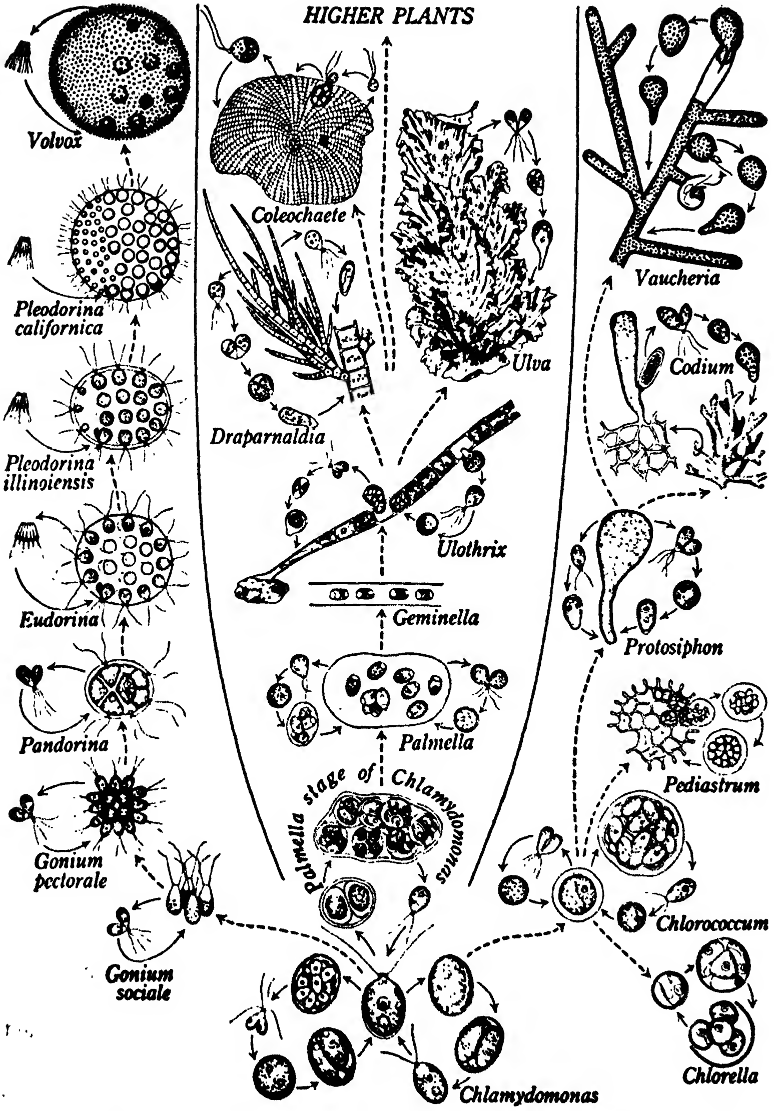


FIG. 565. Diagrammatic representation of the principal lines of evolution in the green algae

Below is *Chlamydomonas*, which may be taken as a type of the ancestral form. To the left various members of the volvocine line are shown successively; the center represents the tetrasporine line, and the right the chlorococcine line

Oedogoniales and in *Spirogyra* and other filamentous members of the *Conjugales*. Owing to the great development of vegetative divisions in the *Ulotrichales*, *Oedogoniales*, and *Conjugales*, these orders are said to show a tetrasporine tendency, and all, therefore, may be included in the tetrasporine green algae.

The third large aggregation consists of forms in which, as in the *Ulotrichales*, the plant is non-motile, and in which motility is found only in reproductive cells. Plants of this third aggregation differ from the *Ulotrichales*, however, in the characteristic absence of vegetative divisions. The simplest forms among them are non-motile unicellular individuals. Related to these are non-motile colonies. Both are included in the order *Protococcales*. While in both unicellular individuals and non-motile colonies there are no vegetative divisions, there may be a division of the nucleus without a division of the protoplast. This tendency toward nuclear division without a division of the protoplast reaches its culmination in the great variety of coenocytic forms in the order *Siphonales*. Among these there is not only great variety in vegetative structures, but also the same variation in sexuality that we find in the other great aggregations; that is, isogamy, heterogamy, and oogamy. The *Protococcales* and *Siphonales* are both included in the protococcine algae.

The great diversity found in each of the three great groups, and the fact that in each there is a gradation from simplicity to complexity, are indicative of three great evolutionary lines among the green algae.

Nature of evidence for evolutionary lines. In our consideration of the green algae it has been indicated that various lines of evolution can be traced from very primitive unicellular green algae, and that these in turn appear to have been derived from green flagellates. When dealing with the development of some of the higher groups of plants we shall be able to trace much of their evolution through the ages by means of fossils. Where the study of the geological history of a group is possible, the evidence thus obtained is invaluable in tracing the course which evolution has taken. In the study of the evolution of the green algae the geological record is practically useless, as the simpler green algae with their small and delicate bodies are very poor objects for preservation. We must therefore depend entirely on a study of living plants, and deduce what inferences we can from a comparison of the various forms. We should remember that in the course of geological time many plants have passed out of existence and that at best we can have only a partial record in living forms. In many cases it must be that ancestral forms which we should like to know have lost out in the struggle for existence, and that in trying to determine what ancestors were like we have to depend on relatives of ancestors rather than on ancestors themselves. In trying to trace ancestry there are many pitfalls. We have noted and shall note again that there have been many cases of parallel development in the plant kingdom. As an example of this we may cite the repeated independent development of oogamy. So it may be that what we may regard as an ancestral form is after all not an ancestral form but one which has resulted from a more or less parallel development. We have also to note that simplicity may not be due to an original primitive condition but may be the result of the simplification of a more complex form; we have seen an excellent example in *Protococcus.* From the above considerations it is evident that we should be very slow in saying that one living form is derived from another. Rather should we conclude that a consideration of a series of forms illustrates the general trend which evolution may have taken. As a concrete example, it would be rash to say that *Ulothrix* and all other *Ulothrichales* are descended from *Chlamydomonas.* The fact that the zoospores of *Ulothrix* and many other green algae have four flagella suggests at least the possibility that they may have been descended from some quadriflagellate unicellular form which in many other respects was closely similar to *Chlamydomonas.* This possibility is emphasized by the fact that there is a unicellular alga (*Carteria*) which differs from *Chlamydomonas* only in having four flagella instead of two.

The evidence, however, does seem sufficiently conclusive for us to decide that most of the green algae have descended either from a *Chlamydomonas* or from forms very similar to that genus, and that we are justified in using *Chlamydomonas* to help us in making a mental picture of an ancestral form for most of the *Chlorophyta.* The study of the lines of evolution is particularly interesting in the green algae because among them we find so many forms which are not only simple but are also, apparently, primitive. The only arrangement of this diversity of forms which seems really logical is one in which various lines of development radiate out from simple forms of which *Chlamydomonas* may be taken as a type.

Origin of lines of development in the green algae. In the life history of the unicellular alga *Chlamydomonas* we see various phases, the development of which appears to have resulted in the conspicuous lines of evolution which we find in the green algae. The dominant phase of *Chlamydomonas* is motile, and the development of this phase appears to have resulted in the formation of motile colonies, culminating in *Volvox*. In this, the volvocine line of evolution, we see the production of larger and larger colonies of cells having many points in common with those of *Chlamydomonas* until the colony of *Volvox* may consist of many thousands of cells. Also, there is a differentiation of vegetative and reproductive cells. In the simpler colonies all cells are reproductive; then there is a form in which a few remain permanently vegetative, followed by a more advanced condition in which about half remain vegetative; and, finally, in *Volvox* the great majority are vegetative while only a few are reproductive.

Under certain conditions *Chlamydomonas* changes from a motile organism to a non-motile one and has a palmella stage. In this non-motile phase vegetative divisions are prominent and motility is suppressed until special motile reproductive cells are formed. The development of such a stage, in which vegetative divisions are prominent, is the tetrasporine line of development, and leads through the *Tetrasporales* to the filamentous and expanded *Ulotrichales*, and probably through these to the higher plants. In the *Ulotrichales* there is a great development of vegetative divisions, a development initiated in the palmella stage of *Chlamydomonas*. Throughout the *Ulotrichales*, however, we see in the production of reproductive cells a return to ancestral characteristics in the method by which the protoplast divides to form reproductive cells, in the flagellated character of each cell, in the occurrence of a single chloroplast, and in the frequent presence of eyespots and contractile vacuoles.

Prior to the production of motile reproductive cells, both zoospores and gametes, *Chlamydomonas* withdraws its flagella and becomes a non-motile individual. This non-motile phase is very different from the palmella stage. It is followed by the production of special motile reproductive cells, whereas the palmella stage is characterized by vegetative division. The prolongation of the non-motile phase preceding the formation of zoospores or gametes, and the omission of the palmella stage, would result in a plant similar to *Chlorococcum*. Such a development appears to have resulted in the *Chlorococcales*, where the dominant phase is non-motile, there are no vegetative divisions, and division occurs only in connection with reproduction. This is the chlorococcine line of evolution. While in the *Chlorococcales* there are no vegetative divisions, there is a tendency toward the development of the multinucleate condition through nuclear division without a division of the protoplast. This tendency seems to have resulted in the production of the complicated coenocytes of the *Siphonales*.

The three lines of development which appear to have originated from the simple unicellular green algae, of which we have taken *Chlamydomonas* as an example, are very different and distinct from each other. However, the development in the three cases has shown certain similar tendencies. In each case we can trace a development from simplicity to complexity; in each there is an increased development and separation of vegetative and reproductive parts; and in each we can trace the development of sexuality from the fusion of isogametes, through the union of heterogametes, to highly developed oogamy, in which a large non-motile egg is fertilized by a small spermatozoid.

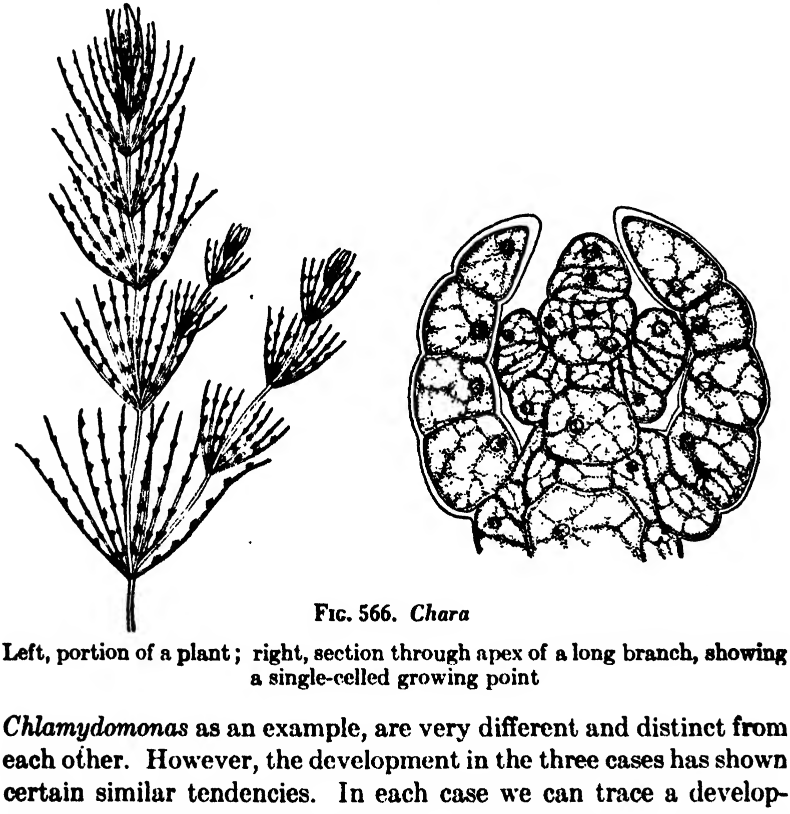


FIG. 566. *Chara*

Left, portion of a plant; right, section through apex of a long branch, showing a single-celled growing point

The green algae afford an excellent example of the tendency of evolution to produce a radiating development and for a simple organism to develop along various lines. The common ancestry of the various lines indicates a similarity in protoplasm which is reflected in each line in the capacity for complex development, in the differentiation of vegetative and reproductive parts, and in the evolution of the differentiation of sexuality.

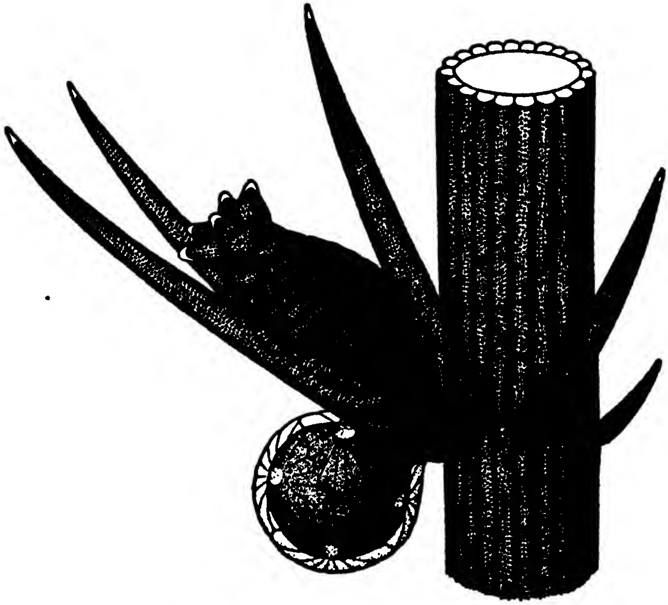


Fig. 567. A branch of *Chara* bearing a large oval oogonium and below this a rounded antheridium. (× 50)

ORDER *CHARALES*

Chara

General characteristics. *Chara* is a highly developed green plant which is common in fresh waters (Fig. 566). The vegetative portion is much branched and is anchored to the substratum by small branched filaments known as rhizoids. The growth of *Chara* in length is due to a single apical cell (Fig. 566). The branches are of three kinds. The main branches are alike and of indeter-

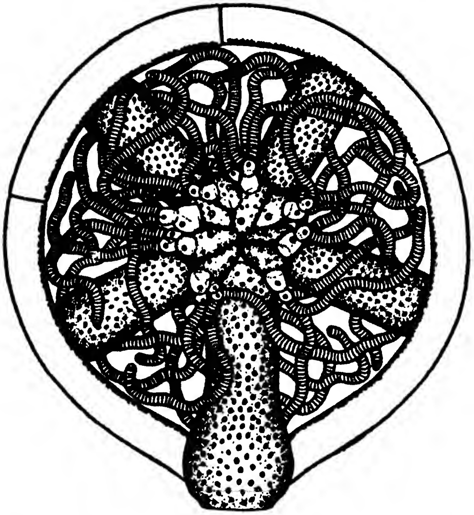


Fig. 568. Section of antheridium of *Chara* showing method of attachment to plant and contents

minate growth. These long branches consist of long internodes and short nodes. The internode is composed of a large long cell surrounded by a single layer of smaller cells which are called cortical cells. A node consists of a plate of cells, and at the nodes there are whorls of short branches of limited growth. The short branches are also composed of nodes and internodes. The internode, like that of the main branch, is composed of a large long cell surrounded by a single layer of smaller cortical cells (Fig. 567). At the nodes of these branches there are unicellular branches and the sexual organs (Fig. 567).

Reproduction. *Chara* does not produce asexual spores, but there may be vegetative reproduction by tuberlike outgrowths or special branches. Sexual reproduction results from the fertilization of eggs by spermatozoids.

The oogonium is egg-shaped, and consists of a cell containing a very large egg (Fig. 567). The oogonium is surrounded by a flask-like jacket of spirally wound cells. The tip of each of these cells is cut off to form a small cell, and the five cells so formed, collectively, make up the crown.

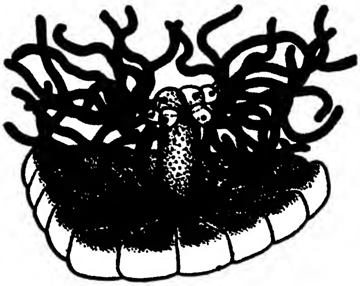


Fig. 569. *Chara*

A shield cell with manubrium projecting from it. At the tip of the manubrium are two head cells to which are attached smaller cells bearing filaments of spermatozoid cells

The antheridium is spherical

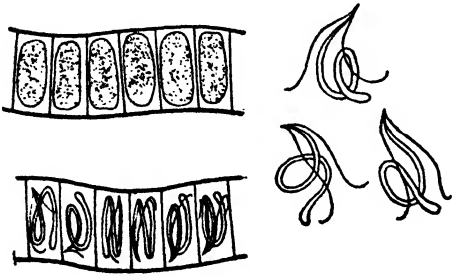


Fig. 570. ***Chara***

Left, portions of two filaments of spermatozoid cells, one showing cells before formation of spermatozoids, the other with contents transformed into spermatozoids; at the right, mature spermatozoids. (× 1000)

(Fig. 567), is red when mature, and has an exceedingly complex structure. It is, in fact, the most complex antheridium in the whole plant kingdom. There is an outer layer consisting of eight cells known as shield cells. From each of these there projects inward a long cell, the manubrium (Figs. 568, 569). At the inner end of the manubrium is a rounded cell, the head cell, which often divides into two. The head cell produces varied numbers of small cells. From each of the ultimate cells there grow long filaments, each of which contains many cells. A spermatozoid is developed in each of these cells (Fig. 570). When an antheridium is mature, it is ruptured and the spermatozoids swim around, some of them reaching oogonia. A single spermatozoid fuses with an egg cell to form an oospore. When an oospore germinates it grows into a new *Chara* plant (Fig. 571). *Chara* shows a high degree of sexual differentiation in that very large non-motile eggs are fertilized by comparatively small spermatozoids. There is, moreover, a high degree of differentiation in the oogonia and antheridia. The oogonia are surrounded by a jacket of sterile cells. The antheridia are particularly complex in that they have a covering of sterile cells and also other supporting sterile cells. The sexual organs of *Chara* are very complex, but at the same time are very favorable objects for study because they are large and the component parts are easily seen. As *Chara* is a very common and widely dis-

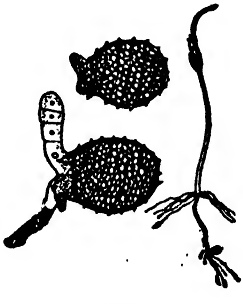


Fig. 571. Stages in the germination of *Characeae*

The two on the left redrawn after De Bary; the one on the right redrawn after Pringsheim tributed plant and exhibits a very high degree of vegetative and sexual differentiation which can be readily demonstrated to students, it has been much used to illustrate a highly developed stage of sexual differentiation. For this purpose it is certainly one of the most beautiful examples among all plants.

Relatives of *Chara*. The *Charales* are a small and very homogeneous group. There is a great similarity in the main characteristics of the group, including reproduction, and they generally differ from each other only in minor details.

Relationship. The *Charales*, of which *Chara* is a very representative and common example, are a very isolated group. Relationship with the green algae is indicated by a bright green color and the storage of food in the form of starch. However, both the vegetative structure and the method of reproduction in the *Charales* are very different from anything known in the green algae. This difference is so great that although the *Charales* may have been derived from the green algae in some way unknown to us, it is generally agreed that the *Charales* should be placed in a different group. Many authorities go so far as to exclude them from the algae on account of their complexity. As their green color and the storage of food in the form of starch indicate a relationship to the green algae, it is convenient to treat them in connection with that division.

CHAPTER XXI

CHRYSOPHYTA AND *PYRROPHYTA*. SOME YELLOW-GREEN AND BROWN THALLOPHYTES

In the last chapter we had a survey of the green algae. That division comprises many and various forms which appear to be clearly derived from simple green flagellates and which are characterized by a bright-green color. In this chapter we will take up plant forms, flagellates and algae, in which the chlorophyll is more or less masked by yellow and brown pigments so that the plants have a yellowish-green, golden-brown, or brown appearance. Most of these forms appear to be related to each other, but they do not form as homogeneous a group as the green algae. All of them are small forms, and the great majority are microscopic.

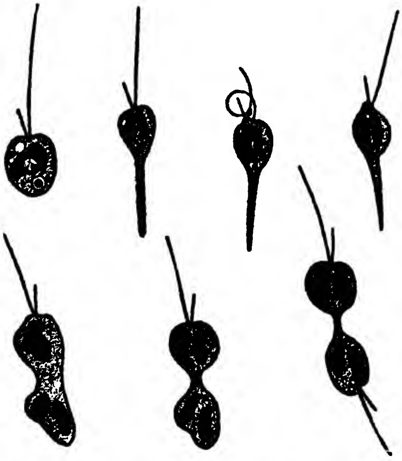


FIG. 572. *Chlorochromonas minuta*

Above, the first two figures show different forms assumed by the flagellate; the other two figures, the capture and engulfing of a bacterium. Lower row, three stages in division. (× 1100). After Lewis

CHRYSOPHYTA

General characteristics. The subdivision *Chrysophyta* is made up of small and mostly microscopic forms. One class, the diatoms, is of importance because although its members are of microscopic size they are very abundant in both fresh and salt water and serve as food for a great variety of small organisms, and indirectly are a very important source of food for the larger aquatic animals which are used by man. Scientifically the *Chrysophyta* are of great interest because they show lines of evolution which appear to start from simple flagellate ancestors and which radiate out in various directions as do the various lines of evolution in the green algae. Just as the ancestry of most members of the green algae can be traced back to primitive unicellular green flagellates, so we can trace the members of the *Chrysophyta* to simple yellowish-green, golden-brown, or brown ancestors (Figs. 572, 578). The various lines of development in the *Chrysophyta* parallel to a great extent those of the *Chlorophyta*, but evidence indicates that evolution in the two divisions has been entirely independent. Types paralleling those of the green algae include forms of various habits, such as motile colonies, palmelloid forms including dendroid colonies (Figs. 573, 580), filamentous forms both branched and unbranched (Fig. 574),

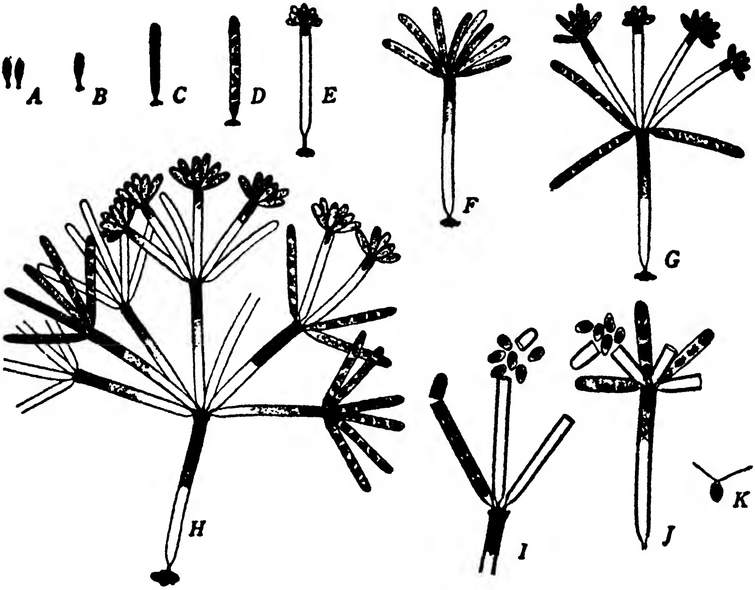


FIG. 573. *Ophiocytium arbusculum*

H, habit. *I*, *J*, escape of zoospores. *K*, zoospore. *A–G*, development of colony from zoospore; the dendroid colony results when zoospores instead of swimming away settle in the open end of the mother cell wall and develop there. (Compare with Fig. 486.) After Braun forms corresponding to the *Chlorococcaceae* among the green algae (Fig. 575), and a siphonaceous genus (Fig. 576), while the diatoms occupy much the same position among the *Chrysophyta* that the desmids do in the *Chlorophyta*.

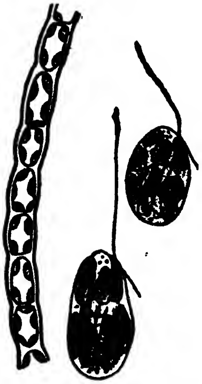


Fig. 574. ***Tribonema***

Left, a filament (after Gay from Oltmanns). Right, zoospores (after Luther)

That the *Chrysophyta* had a common ancestry, and that they are descended from other flagellates than those which gave rise to the *Chlorophyta*, is indicated not only by the way in which many of the *Chrysophyta* can be traced back to simple yellowish-green, golden-brown, or brown flagellates, but also by the fact that there are a number of fundamental characters which are common in the division *Chrysophyta* and which differentiate the *Chrysophyta* from the *Chlorophyta*. The *Chlorophyta* are distinguished by their bright green color, the *Chrysophyta* by the abundance of yellowish-green or brown pigment. The *Chlorophyta* store food in the form of starch, while the *Chrysophyta* do not store food as starch but as oils or leucosin. The cell wall of the *Chrysophyta* is usually composed of two halves one of which fits into the other (Figs. 573, 577), and the walls are often silicified. The flagellated cells of the *Chlorophyta* have flagella of equal length; a considerable proportion of the *Chrysophyta* are characterized by flagella of unequal length, the long one pointed forward and the short one backward.

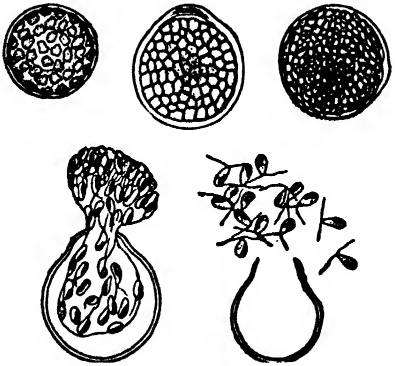


Fig. 575. ***Botrydiopsis arhiza*, a single-celled alga having the same position in the *Chrysophyta* as *Chlorococcum* has in the *Chlorophyta***

The drawing shows an individual and the division of the protoplast to form zoospores. (× 300). After Borzi

It may be that the parallelism between the lines of evolution in the *Chlorophyta* and the *Chrysophyta* exists because the ancestors in both cases belonged to the great group of flagellates. The parallel diversification in the two groups emphasizes the tendency of evolution to spread out in all directions which lie within the limits of the possibilities of the protoplasm of the group. This tendency is further emphasized by the variations within the different classes of *Chrysophyta*. We have seen that in both the bacteria and the blue-green algae evolution has taken place in many directions. The tendency of evolution to produce forms which radiate out in various directions is therefore not peculiar to the *Chlorophyta* and *Chrysophyta*, but

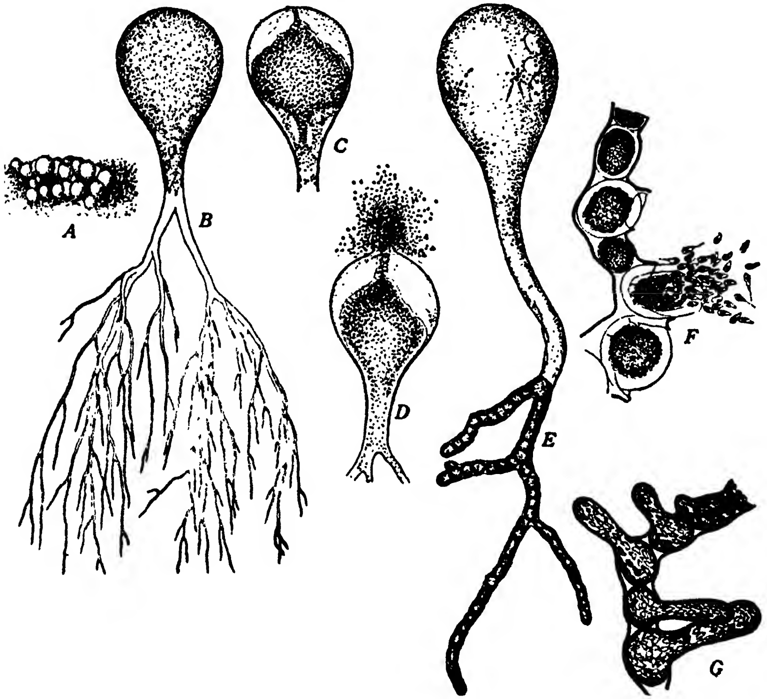


Fig. 576. ***Botrydium***

A, habit sketch (× 2); *B*, an individual, showing balloon-shaped aerial part and branched subterranean portion; *C*, *D*, discharge of zoospores; *E*, formation of hypnospores in underground part; *F*, formation of zoospores from hypnospores; *G*, germination of hypnospores to form new plant. (*C*–*G*, after Rostafinski and Woronin) is in fact a general characteristic of evolution. In the *Chlorophyta* and *Chrysophyta* the radiating lines of evolution are of a higher type than those of the bacteria and blue-green algae, and this may be connected with the more highly differentiated cellular organization.

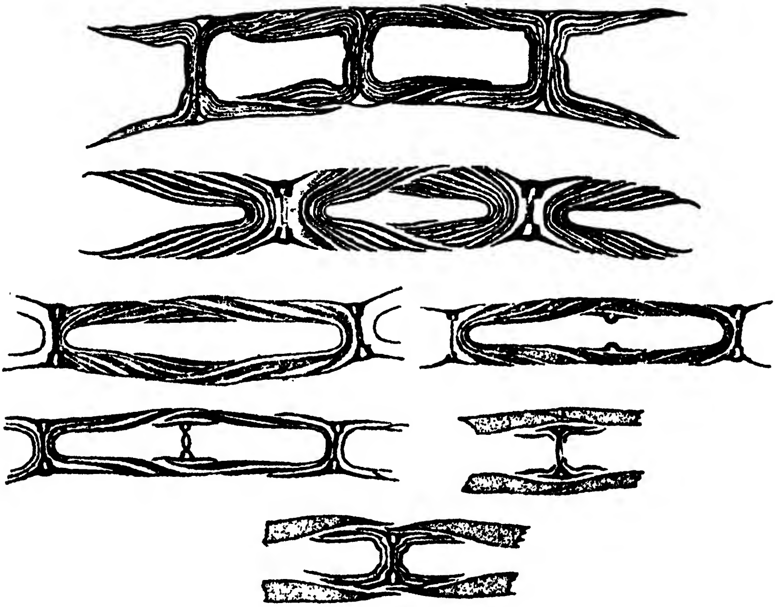


Fig. 577. *Tribonema*

Upper figure, structure of cell wall as brought out by special treatment. The other figures show stages in development of a new section of wall. (× 630). After Bohlin

The *Chrysophyta* are usually regarded as less important than the *Chlorophyta*. It is generally believed that it is among the green algae that we must look for the ancestry of the higher plants, and that the *Chrysophyta* are more of a side line in the evolutionary process.

The *Chlorophyta* are much more prominent in the vegetation of the world than are the *Chrysophyta*. While the *Chlorophyta* contain many common and frequently observed forms, such forms (with the exception of the diatoms) are rare among the *Chrysophyta*.

The division *Chrysophyta* is composed of three classes: *Heterokontae*, or yellow-green algae; the *Chrysophyceae*, a class containing many flagellates and few algal forms; and the *Bacillarieae*, or diatoms.

Class *Heterokontae* (Yellow-Green Algae)

General characteristics. The *Heterokontae*, a diversified group of small organisms, are the class of *Chrysophyta* which most nearly parallel the evolution seen in the *Chlorophyta*. Unicellular motile forms (Fig. 572) and zoospores (Fig. 574) have two flagella of unequal length. Usually the longer flagellum is directed forward and the shorter one backward. The chromatophores are yellowish-green owing to the fact that the chlorophyll is present in small amount while carotinoids are abundant. The chloroplasts usually lack pyrenoids. Reserve food is stored either as oils or leucosin and never as starch. Where there is a definite cell wall, it is usually composed of two overlapping pieces which may be of the same or different sizes (Figs. 573, 577). In filamentous species the wall in longitudinal section appears as composed of a series of overlapping H-shaped pieces (Fig. 577). In reality one piece of wall has the shape of two cups joined together by the bases. Sexual reproduction is found only in a few forms.

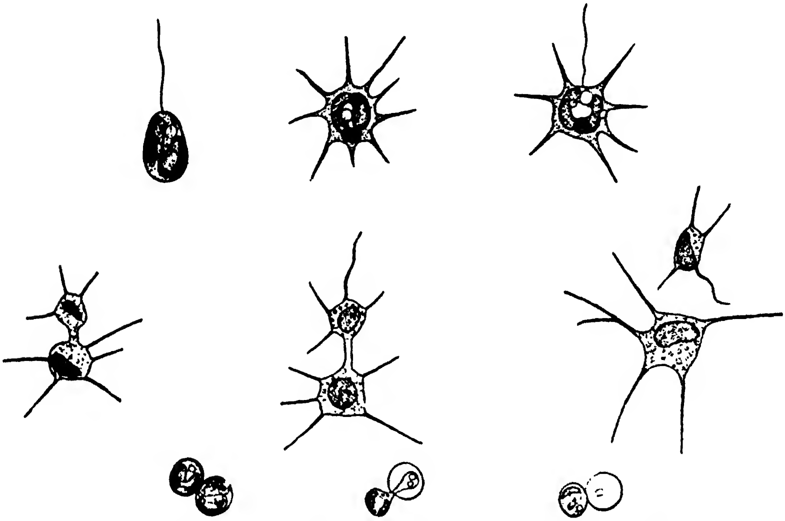


Fig. 578. *Chrysamoeba radians*, one of the *Chrysophyceae*

Upper row, different forms assumed by an individual; second row, stages in division; third row, cysts, and germination of cysts. (× 500). After Scherffel

The most primitive of the *Heterokontae* are unicellular motile forms without cell walls and without sexuality (Fig. 572). In the *Heterokontae*, as in the green algae, we find palmellaceous forms, including both non-motile colonies held together in a gelatinous matrix and dendroid colonies (Fig. 573); filamentous forms (Fig. 574); forms corresponding to the *Chlorococcales* of the green algae (Fig. 575); and a siphonaceous genus (Fig. 576). There are no motile colonies in this class.

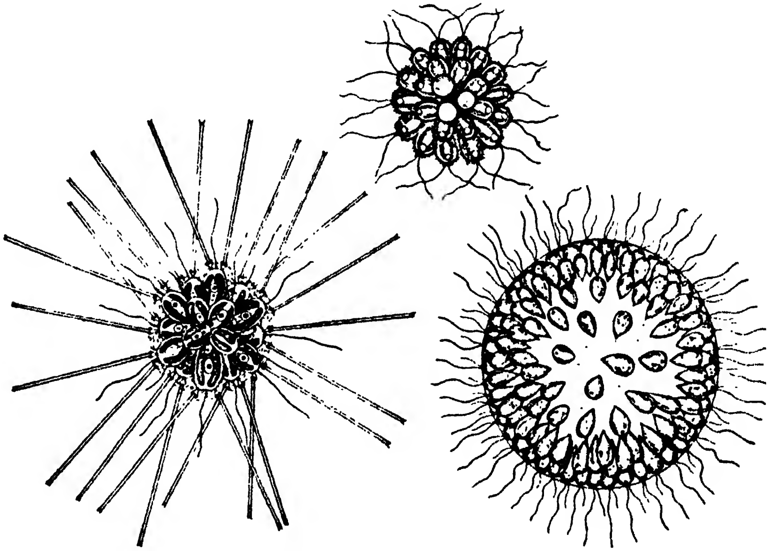


FIG. 579. Colonial *Chrysophyceae*

Left, *Chrysosphaerella longispina*; above, *Synura uvella*; right, *Uroglena volvox*. (After Lauterborn and Stein)

Tribonema. *Tribonema* is a well-known and rather common filamentous genus (Fig. 574). The cell wall has the structure described above for filamentous species (Fig. 577). When cell division occurs an H-shaped piece (as seen in longitudinal section) is formed across the middle of the cell. Layers, which are successively longer and longer, are formed inside the cups until the new piece of wall reaches mature size. Cells are uninucleate and with few to many chromatophores. Asexual reproduction is by aplanospores or by zoospores which are formed singly within a cell. The zoospores have two flagella of unequal length. Sexual reproduction is by the fusion of isogametes.

Botrydium. *Botrydium* is a rather common alga often found in abundance on muddy or damp soil. It is of great interest because it is a siphonaceous member of the *Heterokontae.* The *Botrydium* plant consists of a balloon-like aerial portion which contains the chromatophores and a branched colorless underground part (Fig. 576). In the vegetative plant there are numerous nuclei but no cross walls. *Botrydium* reproduces asexually by the development in the aerial portion of very numerous uninucleate zoospores with flagella of unequal length (Fig. 576 *B–D*); also by the development of aplanospores in the aerial portion and of hypnospores in the underground part (Fig. 576 *E–G*). Sexual reproduction is by the fusion of isogametes.

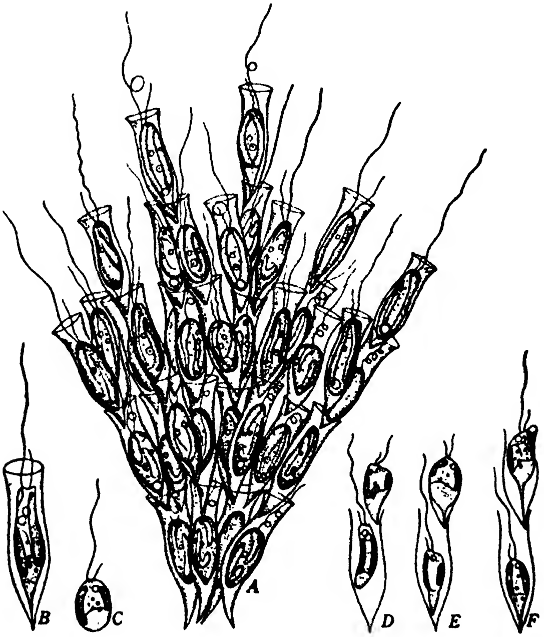


FIG. 580. ***Dinobryon sertularia***

A, habit of colony. *B*, an individual; note the unequal flagella and that the individual is attached at the base to an urn-shaped lorica which is said to contain cellulose and to be somewhat impregnated with silica. Reproduction is by the division of one individual into two and the swimming away of an individual *C* to form a new colony. The dendroid colony is formed by the settling of the individuals in the open mouth of the lorica; *D–F*, formation of new lorica. (After Stein and Klebs)

Class *Chrysophyceae*

General characteristics. The class *Chrysophyceae* is a varied group containing many flagellate forms both unicellular (Fig. 578) and colonial, and only a few algal representatives. Among the flagellate representatives there are both motile colonies (Fig. 579) and colonies which are attached to a substratum (Fig. 580). While the development of algal forms is comparatively slight, there are a sufficient number of forms, and these are diversified enough, to show that evolution in the *Chrysophyceae* has produced very much the same body types as in the *Chlorophyta* and the *Heterokontae*. There are palmelloid forms and a few filamentous types with cellulose cell walls (Fig. 581). Also, there are forms corresponding to the *Chlorococcaceae* in the green algae; but no siphonaceous genera are known.

The chromatophores of the *Chrysophyceae* are golden-brown owing to the masking of the chlorophyll by other pigments. Food is never stored as starch as is the

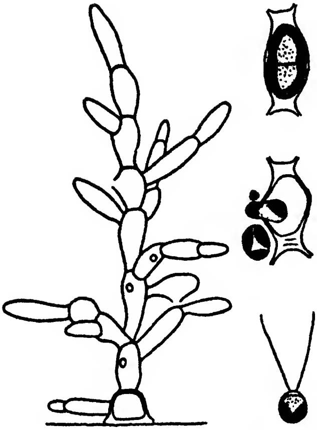


Fig. 581. ***Phaeothamnion confervicalum***

Left, habit of plant. The circular openings are the places from which zoospores have escaped (× 500). Right, development of zoospores (× 900). After Logerheim

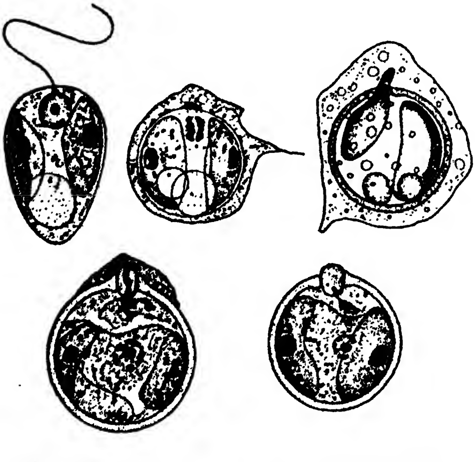


Fig. 582. *Mallomonas pyriformis*, one of the *Chrysophyceae*

A motile individual and stages in the formation of the cyst. (× 500). After Conrad case in the *Chlorophyta*, but rather as oil or leucosin as in the *Heterokontae*. The motile cells may have a single flagellum, two flagella of equal length, or two of unequal length. Those which have two flagella of unequal length resemble the *Heterokontae* in this respect; but in having three distinct types of flagellation the group is distinctive. A very unique character of the class is the formation of distinctive cysts in which the wall consists of two siliceous parts of very unequal size (Figs. 582, 583). One part of the wall is shaped like a flask, the other is very small and is like a stopper in the opening of the flask. The occurrence of walls composed of two parts is indicative of a relationship to the *Heterokontae*, where cell walls are generally of two pieces, one fitting into the other. Sexual reproduction is unknown among the *Chrysophyceae*.

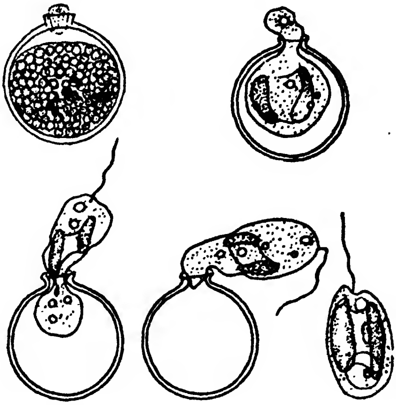


FIG. 583. *Chromulina freiburgensis*

Germination of cyst. (× 435). After Doflein

Class *Bacillarieae* (Diatoms)

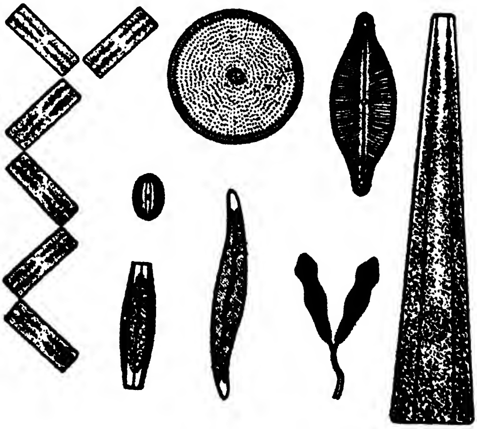


FIG. 584. Forms of diatoms

General characteristics of diatoms. The diatoms occupy a position among the *Chrysophyta* similar to that of the desmids among the *Chlorophyta*. The diatoms are very common aquatic algae, being abundant in both fresh and salt water (Figs. 584, 585). They are distinguished from other plants by their siliceous cell walls, which are in two parts or valves that fit together like the halves of a pill-box. The valves have markings which are often fine and

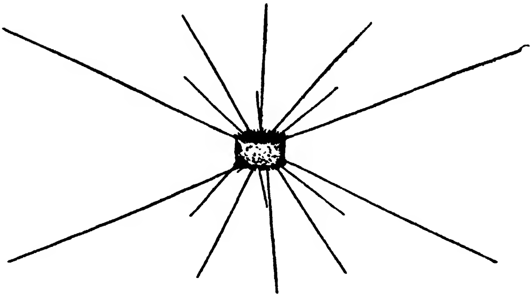


Fig. 585. ***Stephanodiscus hantzschianus*, a diatom with long spines. (× 310)**
After Schröder

beautiful (Fig. 586). The chromatophores are usually golden-brown in color owing to the masking of the chlorophyll by a brown pigment. Diatoms are essentially unicellular plants, but in some species there are simple colonies in which the cells are held together by gelatinous sheaths (Fig. 587). Some of the elongated diatoms have a very distinct gliding movement.

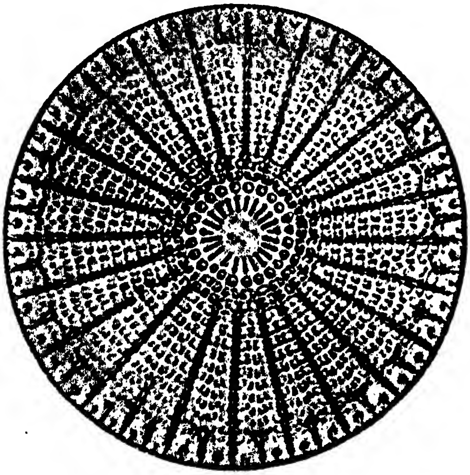


Fig. 586. A diatom cell showing markings
From *Illustrated London News*. (Photomicrograph by Group-Captain C. F. A. Portal, R. A. F.)

Diatoms are usually divided into two orders according to their shape. In the more primitive of the two orders, the *Centrales*, the cell, when viewed from above or below (that is, when looking at the surface of the valve), is radially symmetrical and is often circular. In the *Pennales* the valve is not circular, but is often bilaterally symmetrical. In the *Centrales* the markings on the valves are radial; in the *Pennales* they are often bilateral.

Movement is not found in the *Centrales* with their circular valves, but is restricted to the *Pennales,* which have elongated valves. In those *Pennales* which exhibit movement, there is a long narrow opening or cleft which runs down the center of the valve. Movement is believed to be due to the streaming of protoplasm in this cleft.

Asexual reproduction. The chief method of reproduction among the diatoms is asexual, by the division of one cell into two (Fig. 588). The protoplast enlarges and then divides in two, one daughter protoplast remaining in each valve of the mother cell. Each protoplast then secretes a new valve around the naked half of itself. The new valve fits into the old valve derived from the mother cell. Since one valve of any diatom is slightly smaller than the other and fits into it, the daughter cell formed in the larger valve is of the same size as the mother diatom, while the one formed in the smaller valve is of smaller size; therefore as vegetative reproduction continues there is a tendency for some of the diatoms to become smaller and smaller. The original size is restored by the formation of auxospores. In the *Centrales* this takes place by the separation of the two valves of a cell and the great enlargement of the protoplast, which becomes surrounded by valves rather similar to those of the ordinary vegetative cells (Fig. 589). This auxospore germinates by dividing transversely to form two daughter diatoms (Fig. 589).

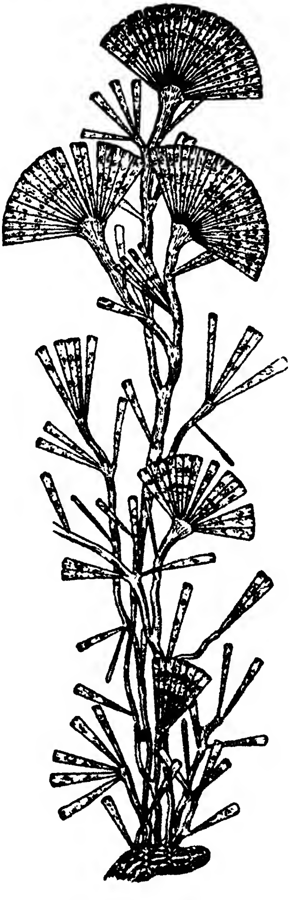


Fig. 587. ***Licmophora flabellata,*** **a colonial diatom.** (× 70)

After Smith

Sexual reproduction. Auxospore formation in the *Pennales* is, at least in many cases, due to sexual fusion (Fig. 590). In some cases the protoplasts of the two diatoms conjugate and form a single auxospore. In other cases two diatoms fuse to form two auxospores. In such cases the two fusing cells become surrounded by a gelatinous envelope and each divides to form two gametes. Each gamete from one of the conjugating diatoms fuses with a gamete from the other conjugating diatom. There are other variations.

In quite a number of the *Centrales* the protoplast is known to divide up to form numerous small flagellated structures which are often called microspores (Fig. 591). These are probably flagellated gametes.

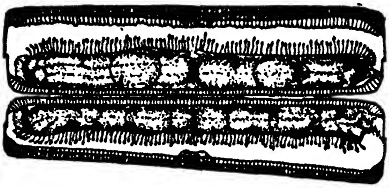


FIG. 588. *Pinnularia viridis*

Two daughter diatoms formed by division. (× 365). After Muller

Relationship of diatoms. The diatoms have several prominent characteristics which indicate a relationship with the *Heterokontae* and *Chrysophyceae* and justify their inclusion in the *Chrysophyta*. These include the brown color; silicified walls composed of two halves, one of which fits into the other; the absence of starch; and the storage of food in the form of oil. The occurrence of flagellated reproductive bodies in many of the *Centrales*, the more primitive order of the diatoms, indicates that the diatoms, like the other *Chrysophyta*, are descended from brown flagellate ancestors. Thus, while the diatoms are very distinct from the *Heterokontae* and *Chrysophyceae*, they possess a number of characteristics that indicate a common origin for the three groups.

The position of the diatoms in the *Chrysophyta* is very similar to that of the *Conjugales* in the *Chlorophyta*. We note particularly many points of similarity between the diatoms and the desmids. Both desmids and diatoms are essentially unicellular. Asexual reproduction is rather strikingly similar in the two cases. In both there is a division of one cell into two, each daughter cell retaining half of the wall of the mother cell. In both the protoplast enlarges and a new half of the cell wall is secreted around the bulging portion of the protoplast. In both desmids and diatoms we find sexual reproduction by the fusion of amoeboid gametes.

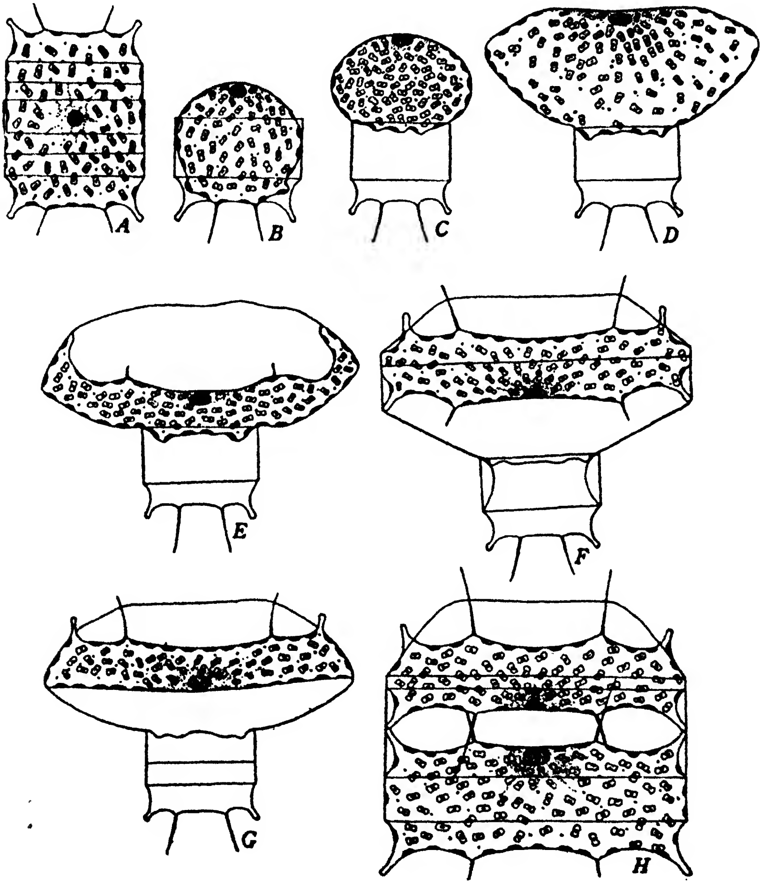


FIG. 589. Auxospore formation in the diatom *Biddulphia mobiliensis*

A, mature diatom; *B*, contents of daughter cell formed by division beginning to escape; *C*, *D*, late stages of escape; *E*–*G*, further stages in auxospore formation; *H*, first division of auxospore. (× 195). After Bergon

When less was known about the evolutionary lines in algae, the similarity between diatoms and desmids led some authorities to place the two in the same class. The differences between the diatoms and the desmids are all very fundamental, and are very characteristic of the *Chrysophyta* and *Chlorophyta* respectively. Thus, the color of the diatoms is brown, that of the desmids bright green. Reserve food stored in the diatoms is oil; in the desmids, starch. The cell wall of the diatoms is of two silicified halves one of which fits into the other; the cell wall of desmids is, as in green algae, of cellulose. A comparison of diatoms and desmids indicates, therefore, that the differences between the two are due to their belonging to distinct groups with separate ancestry. Their similarities can be accounted for by parallel development, which may be taken to indicate a certain similarity in protoplasm. This in turn suggests that while the two may have been derived from different flagellate ancestors, these ancestors themselves were related.

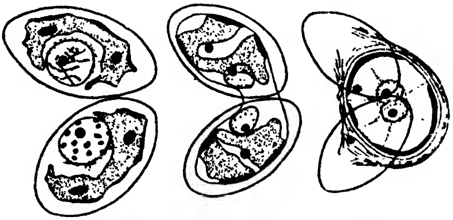


Fig. 590. Stages in conjugation of the diatom *Cocconeis placentula*. (After Geitler)

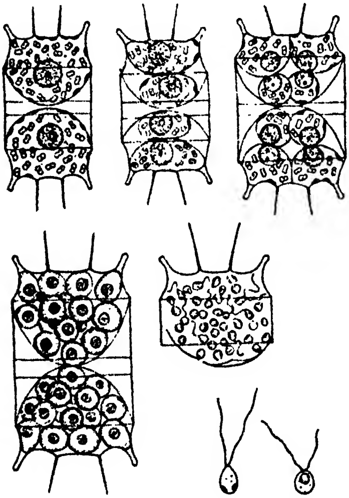


Fig. 591. Microspore formation in *Biddulphia mobiliensis* (× 200) and microspores of *Coscinodiscus oculus*. Compare Fig. 589

After Bergon and Pavillard

When diatoms decay or are digested by animals, the siliceous valves remain, and these fall in considerable quantities to the bottom of a body of water in which diatoms are abundant. Tremendous deposits of diatomaceous earth have been formed in this way. One of the most familiar uses of this material is in scouring preparations; but only a very minor portion of the diatomaceous earth used commercially is employed as scouring material. It is extensively used for filtering and for insulation. It has other important uses.

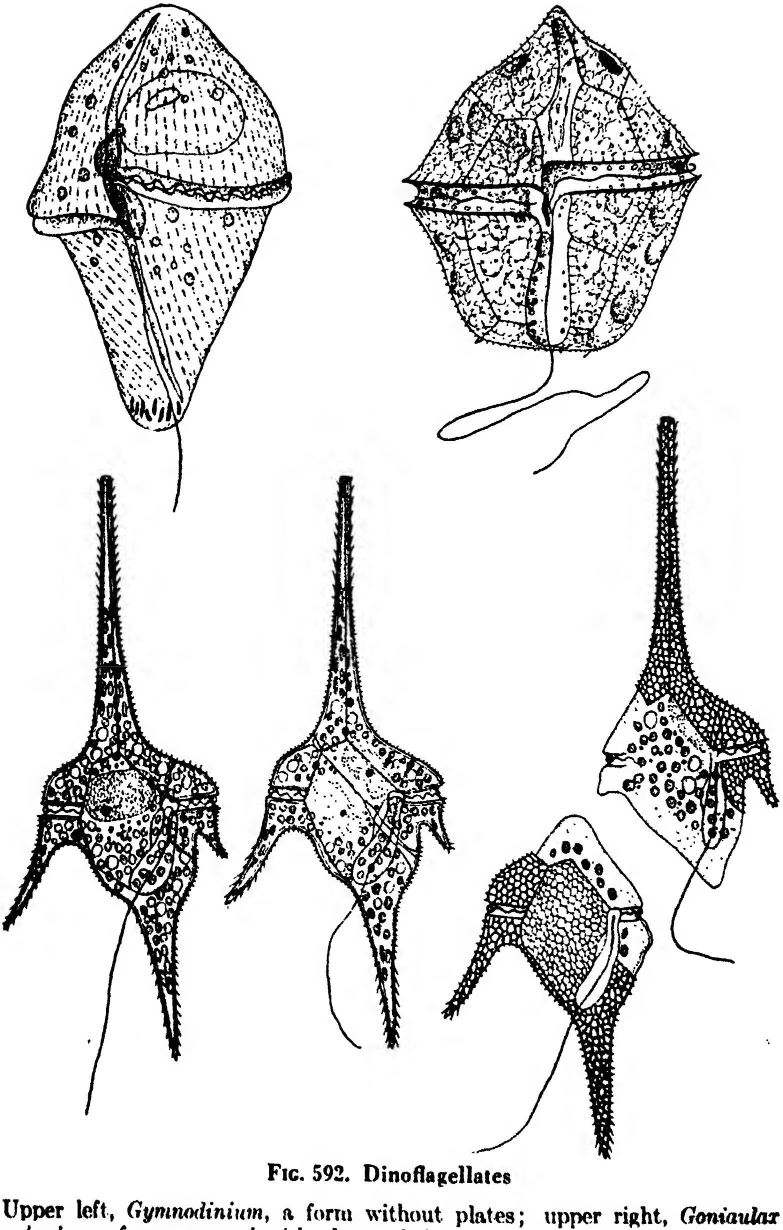


FIG. 592. Dinoflagellates

Upper left, *Gymnodinium*, a form without plates; upper right, *Goniaulax polyedra*, a form armored with plates; below, stages in division of *Ceratium*, showing complete individual, a stage in division, and young daughter cells. After Kofoid-Swezy, Conrad, and Lauterborn

PYRROPHYTA

Class *Dinophyceae*

Systematic position. In this chapter we have just considered the subdivision *Chrysophyta.* The *Dinophyceae* belong to still another division or subdivision, the *Pyrrophyta.* The *Dinophyceae* appear to be derived from or related to a class of flagellates, the *Cryptophyceae,* the two classes forming the division *Pyrrophyta.* The *Dinophyceae* are small organisms with a brown color. They are considered here for convenience and not because they are believed to be closely related to the *Chrysophyta.*

General characteristics. The *Dinophyceae* are typically yellow-brown in color, and the stored food is either starch or oil. The great majority are motile unicellular organisms known as dinoflagellates. A few have naked cells, but nearly all have cellulose walls, which are often in the form of complicated sculptured plates (Fig. 592). A very characteristic feature is the presence of two grooves one of which encircles the cell transversely while the other runs longitudinally along one side. Where the grooves cross each other, two flagella are inserted. One is an undulating strip which lies in the transverse groove; the other runs down a portion of the posterior groove and stretches out behind the cell (Fig. 592). The flagellum in the transverse groove appears to be largely responsible for the rotation of the organism, and the other flagellum for the forward movement. The *Dinophyceae* are remarkable for the very large number of unicellular flagellate forms and the small development of other types. There are, however, unicellular non-motile forms and very simple filamentous ones, and these reproduce by zoospores that have the typical appearance of dinoflagellates. Dinoflagellates reproduce asexually by the division of one cell into two dissimilar halves, after which each half develops anew the missing part (Fig. 592). Sexual reproduction has been reported in one of the *Dinophyceae,* but indications are that it must be of very rare occurrence in the class.

Dinoflagellates are found in both fresh and salt water and are frequently abundant in warmer seas. They are often an important constituent of the floating microscopic flora, and are thus an important source of food for marine animals.

CHAPTER XXII

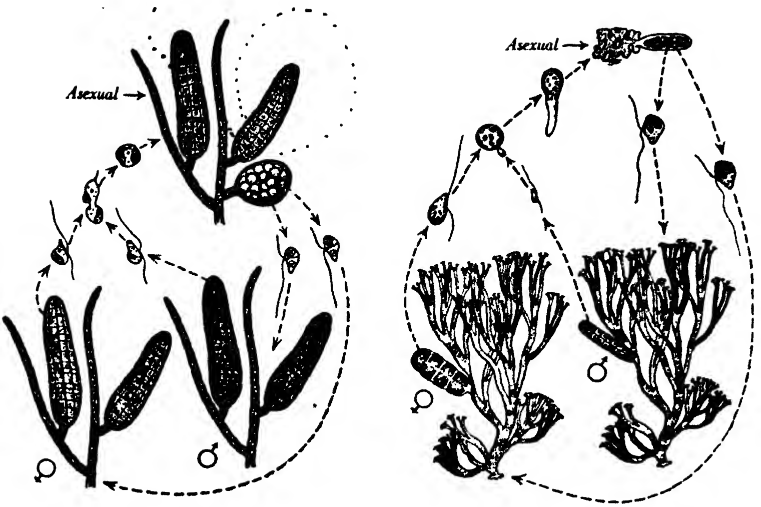
PHAEOPHYTA (BROWN ALGAE)

General characteristics. The brown algae are a very large group of algae with a predominating brown color, from which they get their name. They are nearly all marine. Very simple and primitive forms, which are so numerous in the green algae, are not known among the brown algae. The simplest forms are branched filamentous ones. While many of them are small and filamentous, there are many others which are characterized by large, tough, expanded thalli, and among them there is a great variety of forms. Owing to their large numbers and to the considerable size of many of them, the brown algae are very conspicuous objects along rocky coasts. While they are abundant in the tropics, they are even more prominent in colder waters. The characteristic floating vegetation of the Sargasso Sea (discovered by Columbus, who spent some days in passing through it in 1492) is one of the brown algae, *Sargassum* (Fig. 625). Brown algae are normally attached to a substratum, and it is generally believed that currents bring fresh supplies of floating *Sargassum* to the great whirl of the Sargasso Sea from the coasts toward the southwest. To the brown algae belong the kelps, among which we find the largest of all submerged plants, some of which are many meters in length. Kelps often form immense beds in colder waters; those off the west coast of the United States are well known. Also, in colder waters, brown algae form as a thick covering on rocks exposed by low tides.

Cell structure. The brown algae are multicellular, and each cell is uninucleate. As in the green algae and higher plants, all of the brown algae have a well-developed nucleus and distinct chromatophores. The nucleus, like that of green algae and higher plants, has a definite limiting nuclear membrane and divides by the complicated process of mitosis. The chromatophores, in addition to the ordinary chlorophylls and carotin and xanthophyll found in green algae and higher plants, contain an additional brown pigment called fucoxanthin. The brown color is due to the fact that the brown pigments, carotin, xanthophyll, and fucoxanthin, and particularly the last, mask the chlorophyll. In the brown algae, as in the green algae and higher plants, photosynthesis results in the production of saccharides, and in them food is stored in the form of a polysaccharide or as fat. However, there is the great difference that while in the green algae and higher plants starch (a polysaccharide) is very prominent as a reserve food material, this substance is not known in the brown algae. In them another polysaccharide, laminarin, is prominent.

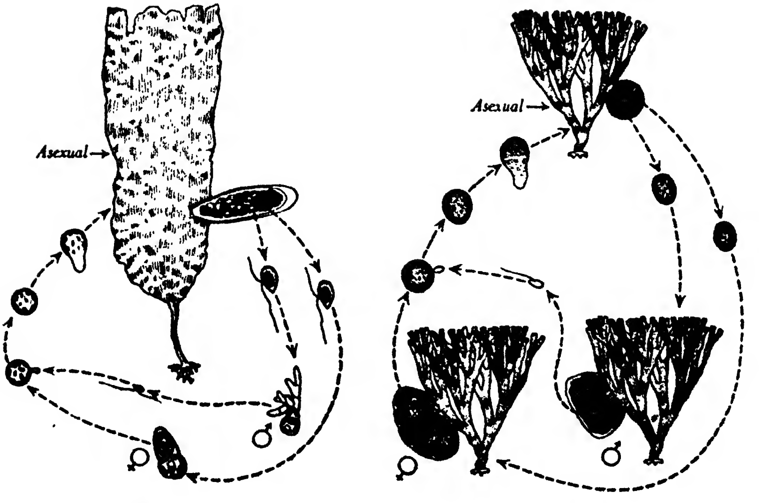
Reproduction. In the simplest of the brown algae sexual reproduction is by the fusion of similar gametes. In some types it is by the fusion of large and small gametes, and in still others by the fertilization of large non-motile eggs by small motile spermatozoids. In the brown algae, therefore as in the green algae, we find various grades of sexual differentiation. Most of the brown algae have an alternation of an asexual generation reproducing by means of asexual spores and a sexual generation which produces gametes (Fig. 593). Typically, the motile cells of the brown algae, whether zoospores, isogametes, heterogametes, or spermatozoids, have two flagella which are attached at the side in such a way that one flagellum is directed forward and the other backward. In some of the brown algae the sexual and asexual generations are alike except in the characters of the reproductive organs and sexual cells. In other cases the sexual plants are large, the asexual ones very much smaller. In still others the asexual plant is large, even of immense size, while the sexual plants are minute; this is true in the kelps. In the *Fucales*, to which the well-known genera *Fucus* and *Sargassum* belong, there are no zoospores, and reproduction is always due to the fertilization of a large non-motile egg by a small spermatozoid. In the brown algae there are no resting reproductive cells, as both zoospores and the cells resulting from sexual fusion germinate without undergoing any period of rest.

The division *Phaeophyta* contains a single class, the *Phaeophyceae*, which different authorities divide into different numbers of orders. For convenience we will discuss five different types, each of which may be considered as representing a different order.



Ectocarpus

Cutleria



Laminaria

Dictyota

FIG. 593. Four types of alternation of generations in the brown algae

Each has one type of asexual plant and two (male and female) of sexual plants. In *Ectocarpus* all plants are alike vegetatively. In *Cutleria* the asexual plants, in *Laminaria* the sexual, are small. *Dictyota* differs from *Ectocarpus* in that small motile spermatozoids fertilize large non-motile eggs

ECTOCARPUS OF THE ORDER *ECTOCARPALES*

General characteristics. *Ectocarpus* is a very common filamentous alga found in salt water. The filaments grow in tufts and branch profusely (Figs. 594, 595). The numerous slender brown filaments give the plants a soft fuzzy appearance, and as they occur in nature they often form a dense fuzzy coating over the substratum on which they grow.

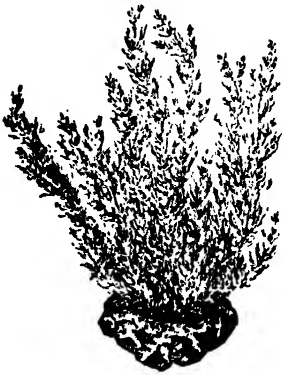


Fig. 594. *Ectocarpus siliculosus.* (× ½)

Sexual reproduction. In *Ectocarpus* there is an alternation of a sexual generation, reproducing by means of gametes which are very much alike, and an asexual generation which produces zoospores (Fig. 593). In vegetative structure the two types of plants are alike. The sexual plants are haploid and produce gametes. These are formed in elongated structures known as gametangia (Fig. 596). A gametangium is composed of many small cubical cells in each of which a gamete is formed. The gametangium is called a multilocular gametangium because it contains many cells or locules. In common with other motile cells among the brown algae, each gamete has two laterally inserted flagella, one of which is directed forward and the other backward. The sexual plants all look alike, even including the gametangia and the gametes. Actually there are two kinds, one producing male gametes and the other female gametes. There may be a difference in size in the gametes produced by male and female plants, the female gametes being slightly larger than the male. The difference, however, is shown in activity rather than in structure, male gametes being attracted to a female gamete (Fig. 597). A number of male gametes may cluster around a single female gamete. Finally a male gamete fuses with the female gamete.

Asexual reproduction. The resulting zygote formed by the fusion of a male and a female gamete germinates to produce an asexual plant. This asexual plant is diploid, and in vegetative structure is exactly like the sexual plant, but produces zoospores. These are of two kinds, formed in two different types of zoosporangia (Figs. 595, 598, 599). One type of zoosporangium is like the gametangia of the sexual plants and is composed of many cubical cells. This type is known as a plurilocular zoosporangium. A zoospore is formed in each cell (Fig. 598). These zoospores are diploid, and on germination give rise to other asexual plants like the one on which they were produced. It is not uncommon to find asexual *Ectocarpus* plants bearing only plurilocular zoosporangia;

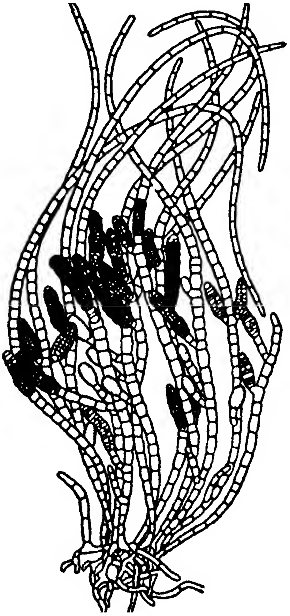


Fig. 595. ***Ectocarpus cylindricus*, an asexual plant with two kinds of sporangia. (× 45)**

After Setchell and Gardner

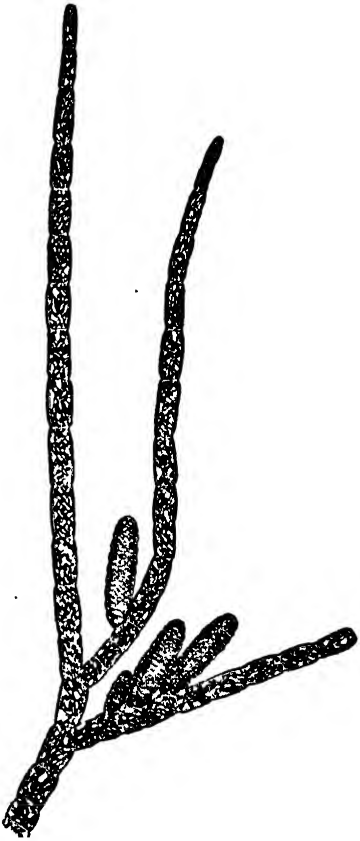


Fig. 596. ***Ectocarpus* with multilocular gametangia. (× 145)**

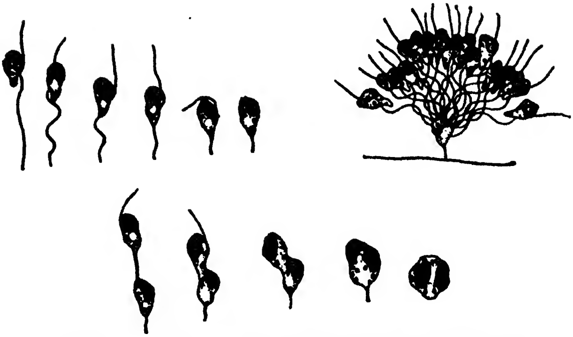


FIG. 597. Fertilization in *Ectocarpus siliculosus*

Upper left, attachment of female gamete; upper right, many male gametes attached to a female gamete; below, fusion of male and female gametes. (× 700). After Berthold

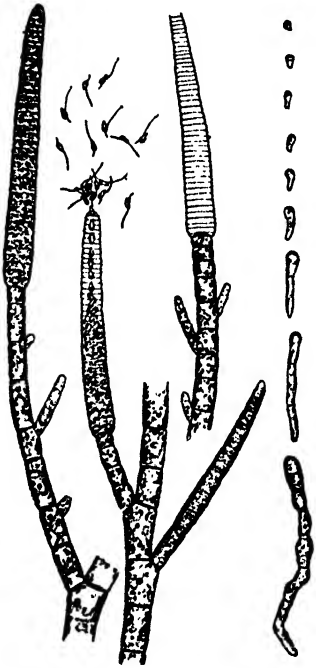


FIG. 598. *Ectocarpus siliculosus*

Left, zoospores formed in plurilocular zoosporangia and escaping; right, germination of zoospore. (× 250). After Thuret

and, as these zoosporangia have the same structure as the gametangia of sexual plants, it is not possible by looking at them to distinguish such asexual plants from sexual ones. The other type of zoosporangium is one cell, usually terminating a small branch, within which a number of zoospores are produced (Fig. 599). This type is called unilocular because it is not divided up by cell walls as is the plurilocular zoosporangium. The first divisions of the nucleus of the mother cell of the unilocular zoosporangium are meiotic or reducing divisions, so that the zoospores produced in the unilocular zoosporangia are haploid. They produce haploid sexual plants, completing the alternation of generations.

In the life history of *Ectocarpus* there is, as outlined above, an alternation between gametophytic plants, some producing male gametes and others female, and sporophytic plants which produce diploid zoospores and haploid zoospores. There are various complications in the life history of *Ectocarpus* which interfere with the strict alternation of gametophytic and sporophytic plants. The sporophytic plants may reproduce indefinitely by the production of diploid zoospores. The gametes from the haploid gametophytic plants may germinate parthenogenetically; that is, instead of fusing, they may act as zoospores and germinate directly to form other gametophytic plants. Thus the gametophytic generation, like the sporophytic one, may be prolonged indefinitely. The haploid zoospores formed in unilocular sporangia may act as gametes and fuse to give rise to diploid gametophytic plants. In such a case the gametophytic generation is omitted.

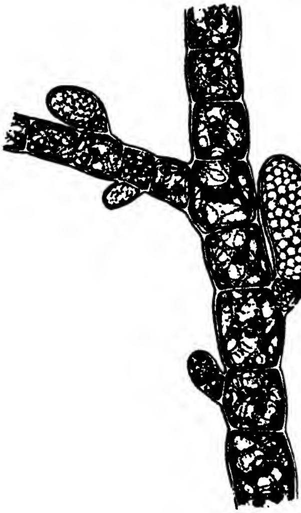


Fig. 599. Unilocular sporangium of *Ectocarpus*. (× 325)

CUTLERIA OF THE ORDER *CUTLERIALES*

General characteristics. *Cutleria* (Fig. 593) is very interesting on account of the type of the alternation of generations which it shows and because the male and female gametes are very different in size (heterogametes). The plants of the sexual and asexual generations are so different from each other not only in size but also in structure and appearance that they were regarded as being different and unrelated plants; and it has only been in comparatively recent times that they have been shown to be simply the sexual and asexual generations of the same plant. In the sexual generation there are two kinds of plants, male and female, which are alike except for comparatively slight differences connected with the gametangia (Fig. 600). The sexual plants are of fair size and with many branches, while the asexual plant is a small flat thallus which is lobed rather than branched.

Sexual reproduction. The gametes are produced in gametangia found in hairy patches on the sexual plants (Fig. 600). The male gametangia, found on male plants, are elongated structures bearing considerable resemblance to the plurilocular gametangia of *Ectocarpus*. They are borne in large numbers on much-branched filaments. The female gametangia,

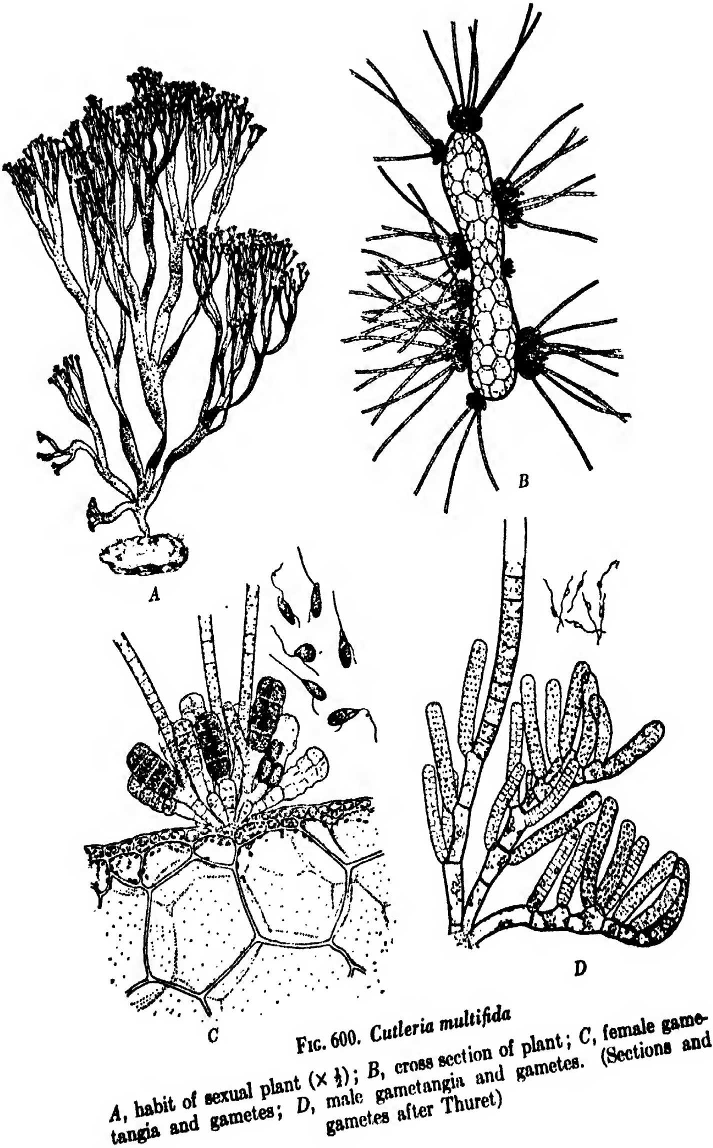


FIG. 600. *Cutleria multifida*

A, habit of sexual plant (× ½); *B*, cross section of plant; *C*, female gametangia and gametes; *D*, male gametangia and gametes. (Sections and gametes after Thuret)

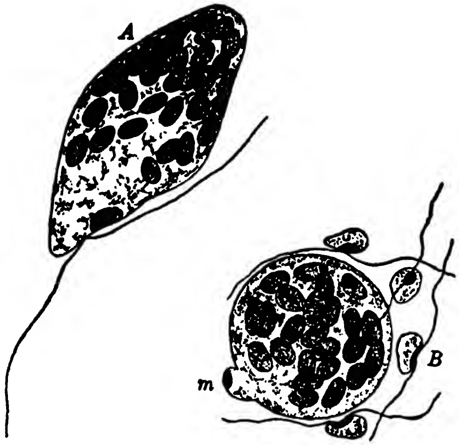


FIG. 601. *Cutleria multifida*

A, the large female gamete; *B*, the same at rest and surrounded by small male gametes, one of which, *m*, is shown in the act of fusion

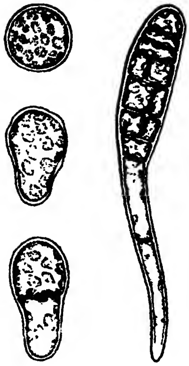


FIG. 602. Zygote of *Cutleria multifida* and its germination

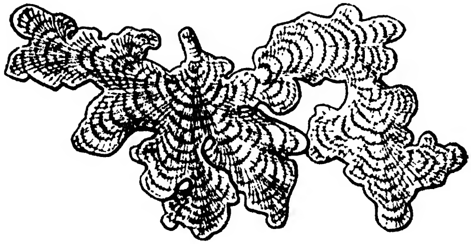


FIG. 603. A young asexual plant of *Cutleria multifida* grown in a culture. (× 75)

After Falkenberg

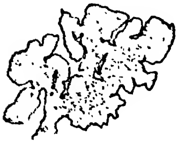


FIG. 604. *Cutleria multifida*

Asexual plant. (Natural size)

produced by female plants, are much stouter than the male and produce comparatively few gametes. Both male and female gametes are biflagellate. The female gametes are very much larger than the male gametes. The difference is so great that in size the female and male gametes are like eggs and spermatozoids. The zygote formed by the fusion of female and male gametes (Fig. 601) germinates (Fig. 602) to produce the small asexual plant (Figs. 603, 604).

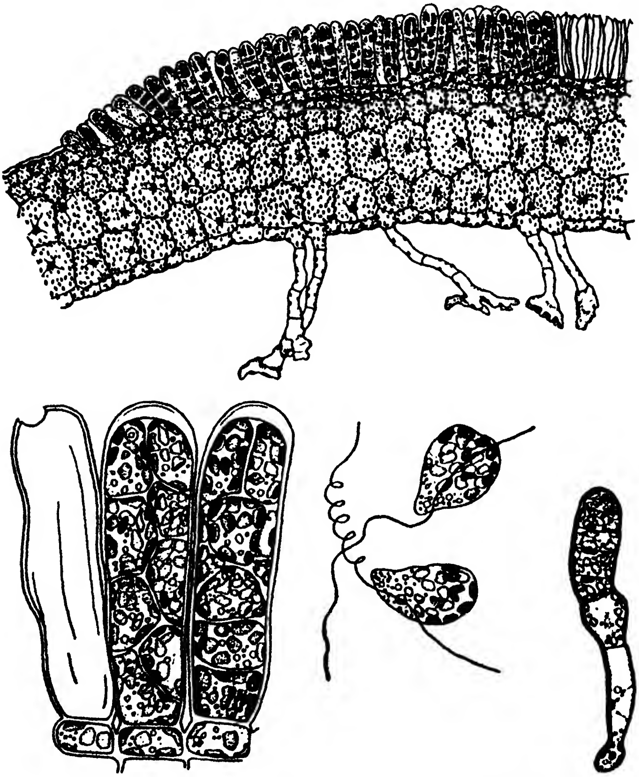


Fig. 605. Asexual plant of *Cutleria multifida*

Above, section showing zoosporangia at upper surface (× 130); below, zoosporangia (× 665), zoospores (× 800), and germination of zoospore. (After Kuckuck)

Asexual reproduction. The zoospores are formed in elongated saclike sporangia which are produced in large numbers on the upper surface of the small asexual plant (Fig. 605). When these zoospores germinate, they give rise to male and female plants.

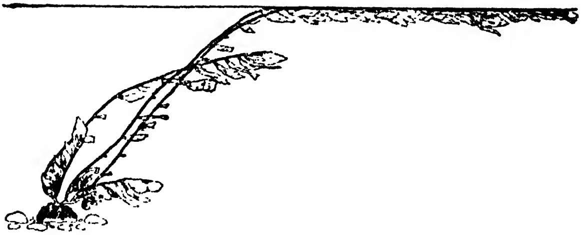


Fig. 606. *Macrocystis pyrifera*, the longest of the brown algae
After Skottsberg

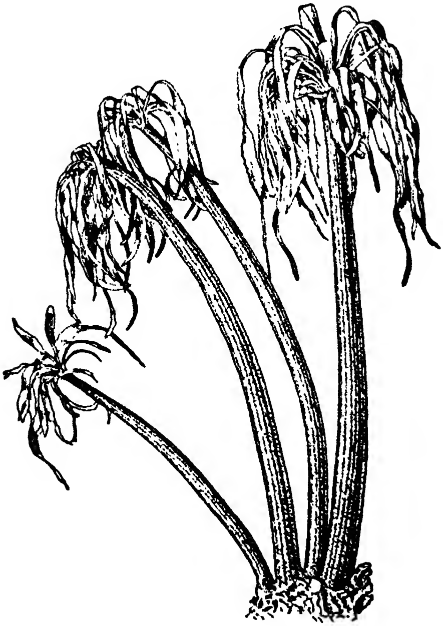
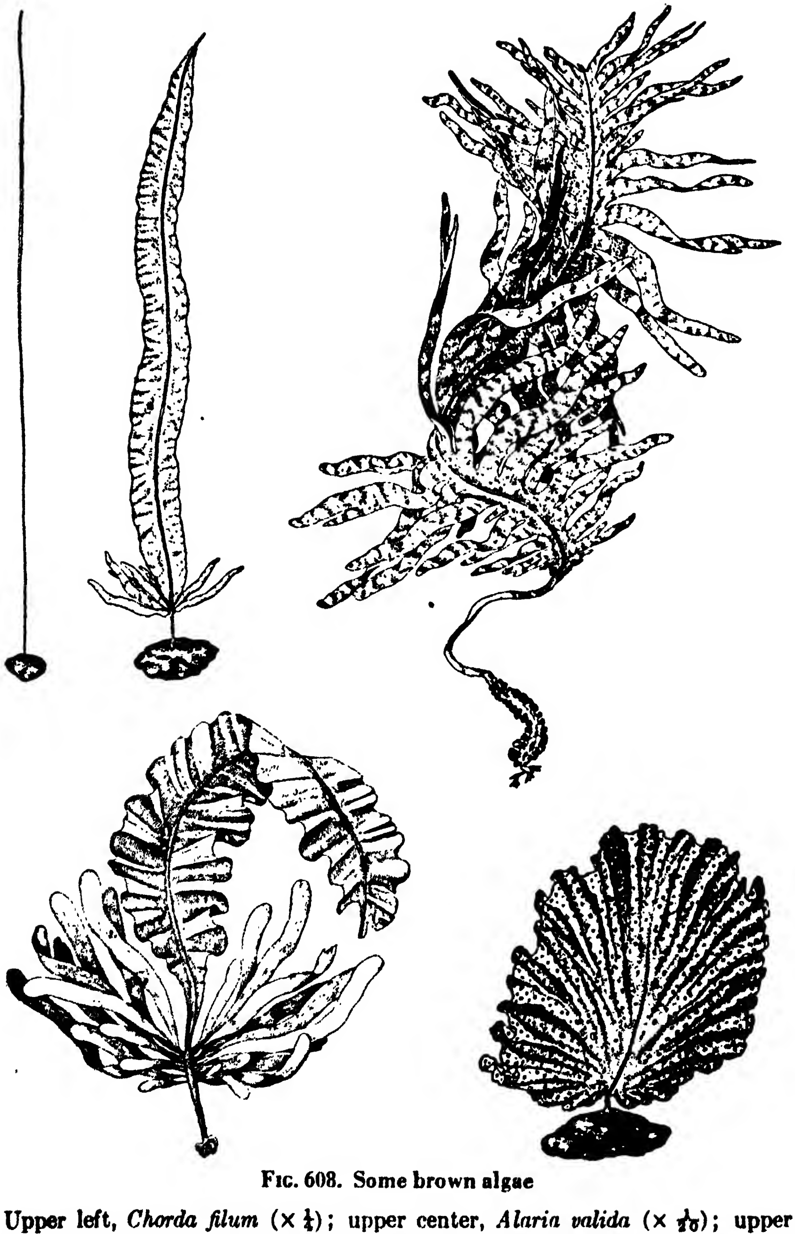


Fig. 607. *Postelsia palmaeformis*. $(\times\frac{1}{10})$
Drawn from a photograph by Setchell and Gardner



Fɪɢ. 608. Some brown algae

Upper left, *Chorda filum* ($\times \frac{1}{4}$); upper center, *Alaria valida* ($\times \frac{1}{20}$); upper right, *Ulopteryx* ($\times \frac{1}{10}$); lower left, *Alaria dolichorhachis*; lower right, *Agarum cirrosum* ($\times \frac{1}{12}$). *Ulopteryx* is much used by the Japanese as food. (*Alaria dolichorhachis* after Kjellman)

LAMINARIA OF THE ORDER *LAMINARIALES*

Kelps. The *Laminariales* are popularly known as kelps. Among these we find the largest and stoutest of seaweeds, some of them many meters in length. The longest of them are composed of long, stout cordlike structures with leaflike branches (Fig. 606). Among the kelps we also find treelike forms (Fig. 607), and many other interesting types of large stout plants (Fig. 608). The genus *Laminaria* is a large and prominent genus of the *Laminariales*, or kelps. Some species of *Laminaria* consist of long expanded sheets with a stout basal cord which is held to the substratum by a stout holdfast. Other species have branched thalli (Fig. 609).

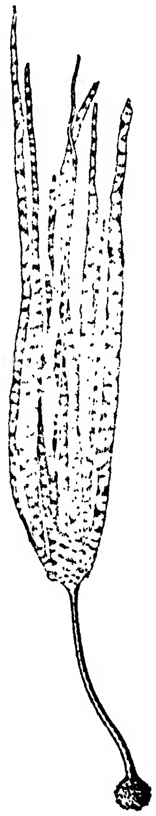


Fig. 609. *Laminaria dentigera*
Modified after Kjellman

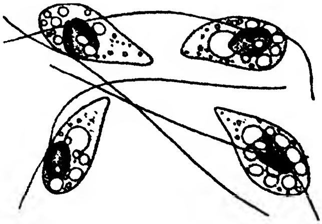


Fig. 610. Zoospores of *Laminaria saccharina*. (× 1200)
After Kuckuck

Asexual reproduction. The *Laminariales* show a very interesting type of alternation of generations (Fig. 593). They differ from any of the plants which we have considered in that the asexual generation is a large plant while the plants of the sexual generation are minute. The large conspicuous plant (Fig. 609) of *Laminaria* is, then, the asexual generation, and is diploid. It produces haploid

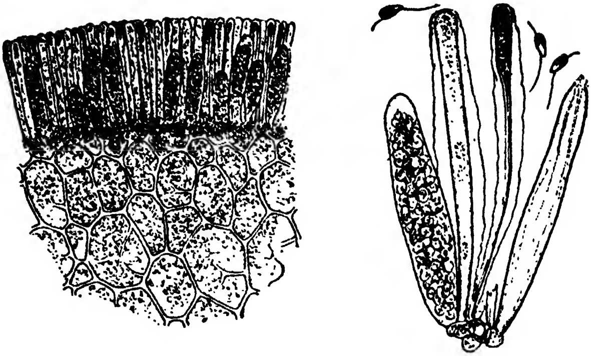


FIG. 611. *Haligenia bulbosa*

Left, portion of a thallus showing sporangia among sterile filaments, the paraphyses; right, sporangia, paraphyses, and zoospores. (After Thuret)

zoospores (Fig. 610) in cylindrical sporangia which occur in vast numbers on the surface of the thallus (Fig. 611).

Sexual reproduction. As the zoospores are haploid, they give rise to haploid plants, some of which are male and others female. Both male and female plants are minute (Fig. 612). The male plants are small filaments which bear antheridia that produce spermatozoids. The female plants consist of only a few cells, sometimes only one; any cell may become an oogonium and produce a large non-motile egg. A spermatozoid fertilizes an egg, and the resulting zygote germinates to produce the large asexual plant.

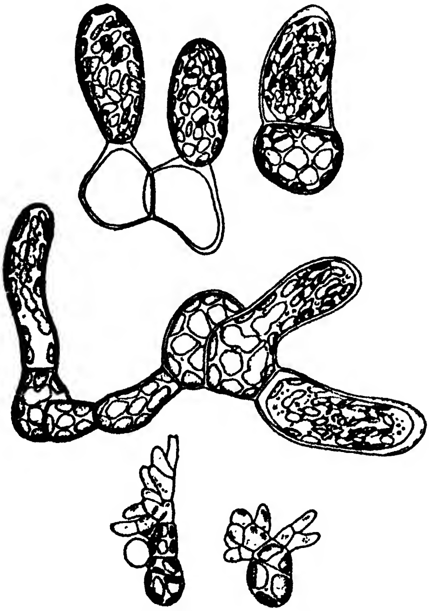


FIG. 612. *Laminaria saccharina*

Above and center, female plants with oogonia; below, male plants with antheridia. (× 600). After Kuckuck

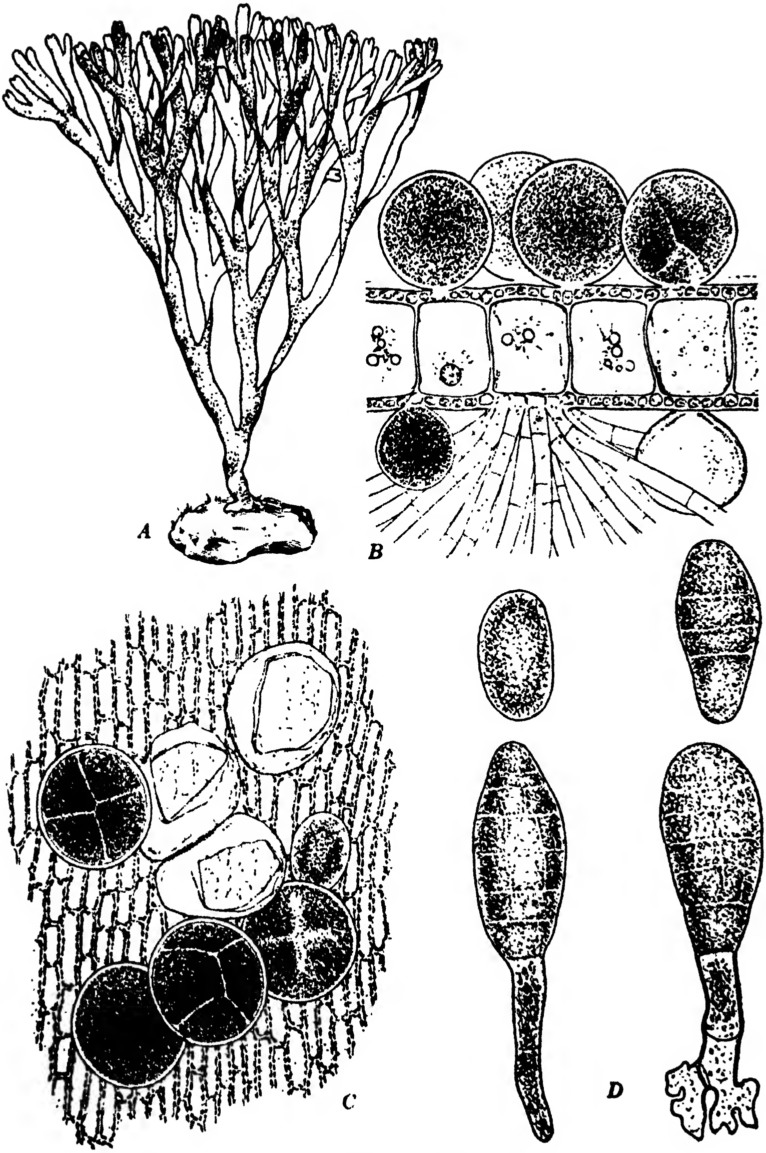


Fig. 613. ***Dictyota dichotoma***

A, habit of plant (× ½); *B*, section through tetrasporangia showing stages in formation of tetraspores; *C*, surface view of thallus with tetrasporangia from some of which tetraspores have escaped; *D*, germination of tetraspores. (All except habit after Thuret)

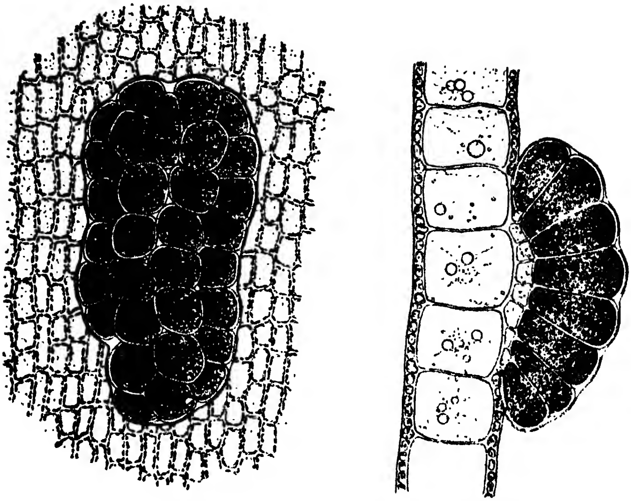


Fig. 614. *Dictyota dichotoma*

Surface view and section through thallus bearing oogonia. (After Thuret)

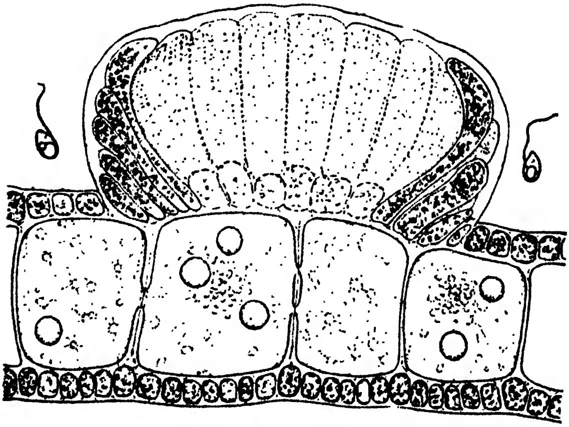


Fig. 615. *Dictyota dichotoma*

Section through thallus bearing antheridia; also spermatozoids. (After Thuret and Williams)

DICTYOTA OF THE ORDER *DICTYOTALES*

General characteristics. One of the most interesting features of the brown algae is the diversity of types of alternation of generations found in the different orders. In *Dictyota*, as in *Ectocarpus*, both generations are alike in vegetative structure (Fig. 593); but *Dictyota* differs in various features. In it large non-motile eggs are produced by female plants and small motile uniflagellate spermatozoids by male ones. A *Dictyota* plant is a flat dichotomously branched thallus with ribbonlike branches (Fig. 613).

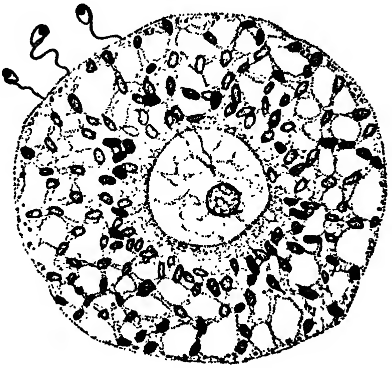


FIG. 616. *Dictyota dichotoma*

Section through egg. Three of the many spermatozoids which were attached to it are drawn. Note difference in size between egg and spermatozoid. (After Williams)

Sexual reproduction. In the sexual generation of *Dictyota* there are two kinds of plants, male and female. The female plants produce eggs in single-celled oogonia which occur in patches on the surface of the thallus (Fig. 614). Spermatozoids are formed in tremendous numbers in groups of antheridia which are found on the surface of the male plants (Fig. 615). The eggs and spermatozoids are discharged into the water, and an egg is fertilized by a spermatozoid (Fig. 616). As in other brown algae with an alternation of generations, the plants of the sexual generation are haploid as the gametes are, while the fertilized egg is diploid.

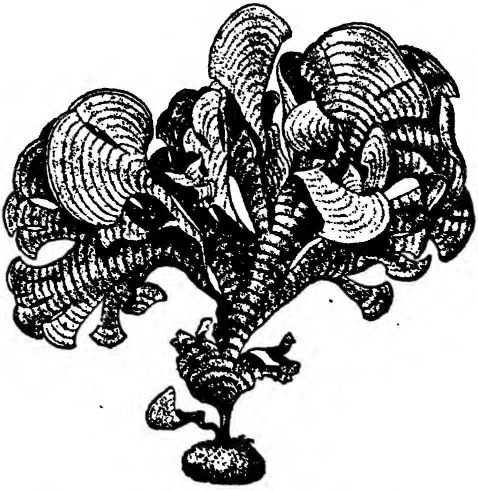


FIG. 617. *Padina australis*, a relative of *Dictyota*. (× ⅔)

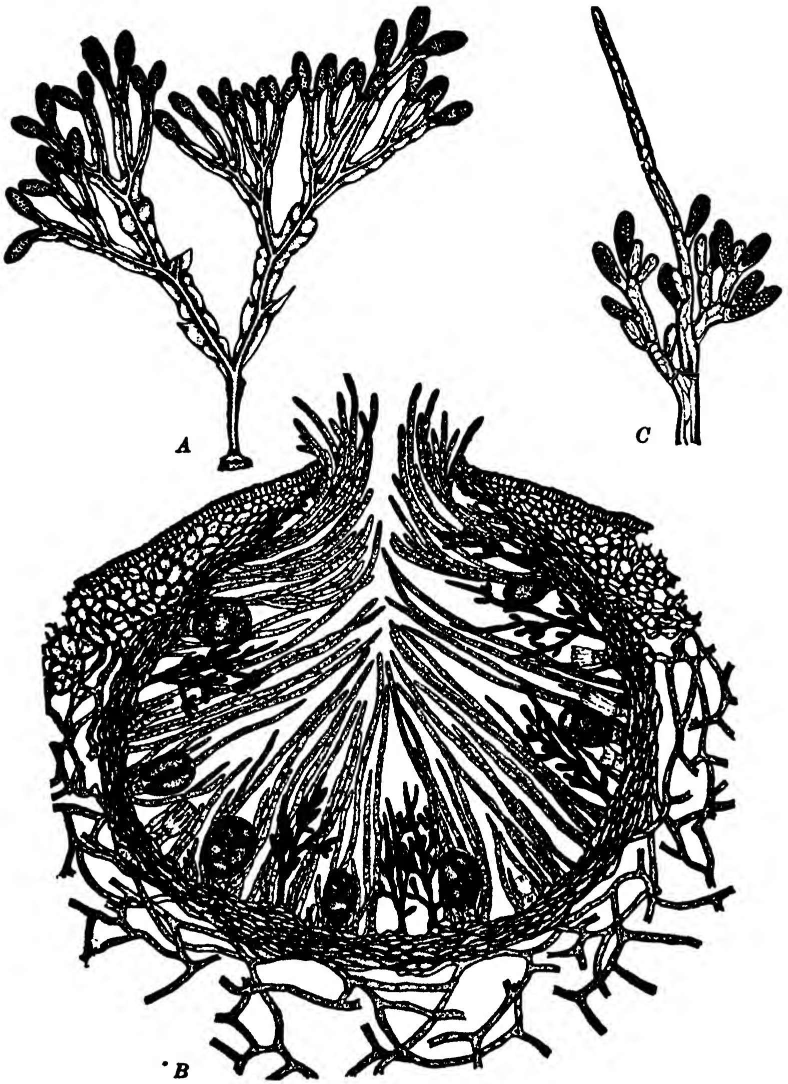


FIG. 618. *Fucus*, a brown alga

A, complete plant, showing holdfast attached to rock and expanded fertile tips of thallus (× ½). The dots in the fertile tips are openings into flask-shaped conceptacles containing gametes (eggs and spermatozoids; whether in the same conceptacles or on different plants depends on the species). *B*, section of conceptacle showing branched antheridial filaments and oval oogonia, each when mature containing eight eggs (× 65). *C*, antheridial filament with numerous antheridia, each containing many spermatozoids (× 160)

Asexual reproduction. The fertilized egg germinates to produce a diploid asexual plant. The spores produced by these asexual plants are very different from those found in other orders of brown algae (Fig. 613). We have seen that in *Ectocarpus*, *Cutleria*, and *Laminaria* the asexual spores are biflagellate zoospores. In *Dictyota* the asexual spores are large non-motile ones which are known as tetraspores. They get their name from the fact that four of them are produced in a sporangium. The sporangia are known as tetrasporangia; they are large rounded structures found in patches on the surface of the thallus of an asexual plant. On germination the tetraspores give rise to sexual plants, some of which are male and others female. Meiosis occurs during the nuclear divisions in the tetrasporangium, so that the tetraspores are haploid.

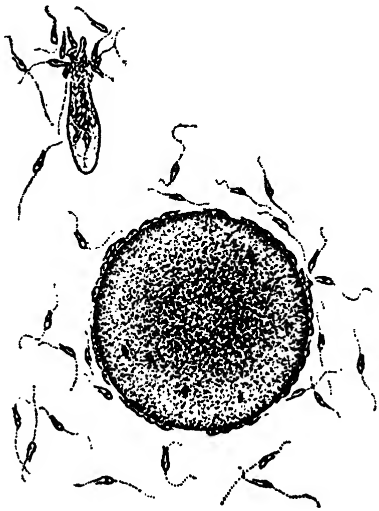


FIG. 619. ***Fucus vesiculosus***

Above, antheridium from which spermatozoids are escaping; and below, a single egg surrounded by many spermatozoids. (× 330). After Thuret

FUCUS OF THE ORDER *FUCALES*

General characteristics. The genus *Fucus* is a very common marine alga, widely distributed in colder waters (Fig. 618). The *Fucales* differ from the other orders of brown algae in that they do not produce asexual reproductive cells, reproduction being always due to the fertilization of an egg by a spermatozoid (Fig. 619). There is therefore no alternation of distinct asexual and sexual plants. A *Fucus* plant consists of a flattened, dichotomously branched thallus with a stout basal stipe connecting the expanded thallus to the stout holdfast. In the thallus of some species there are swollen places or bladders which are filled with air. The tips of the branches are also swollen, and it is in these swollen tips that reproductive cells are produced. They are found in flask-shaped structures known as conceptacles which are embedded in the swollen tips. Numerous unbranched multicellular sterile hairs known as paraphyses grow from the lining of the conceptacle into the cavity. Among these are found the oogonia and antheridia (Fig. 618).

Reproduction. Depending on the species, both oogonia and antheridia may be found in the same conceptacle, or all conceptacles of one plant may contain only oogonia or only antheridia. In the first case the plants are bisexual (that is, they produce both male and female reproductive cells); in the second, the plants are unisexual and are of two kinds, male and female.

The antheridia are oval saclike structures which are borne in considerable numbers on much-branched special filaments (Fig. 618). The antheridia contain a large number (sixty-four) of spermatozoids (Figs. 619, 620). The oogonium consists of a stalk cell and the oogonium proper. An oogonium is formed from a single cell, and when ripe contains eight eggs (Figs. 618, 621).

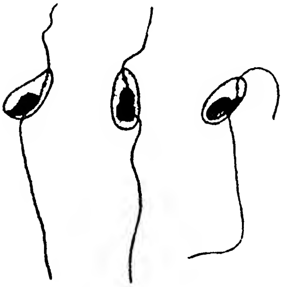


Fig. 620. Spermatozoids of *Fucus*. (× 1100)

After Kylin

The oogonium when young has a single nucleus. This nucleus divides to form eight nuclei, and then the protoplast divides up to form eight eggs, each containing one of the nuclei. The eight eggs are surrounded by the wall of the mother cell (Fig. 621). The antheridium, like the oogonium, starts as a single cell. Its nucleus divides to form 32 nuclei, and the protoplast then divides up to form 32 parts, each containing one of the nuclei. There is one more division, and this results in the formation of 64 spermatozoids. When the antheridium ripens, the outer part of the wall dissolves at the tip, and the spermatozoids in one mass still surrounded by the inner layer of the antheridium wall are discharged through the opening in the outer layer; finally one end of the inner layer of the wall dissolves and the spermatozoids are set free. Likewise when the eggs are discharged they are in one mass still surrounded by the two inner layers of the oogonium wall; the outermost of these membranes goes to pieces at the tip end, and the eggs in one mass still surrounded by the innermost membrane escape; one end of the innermost membrane then goes to pieces, and the eggs are set free. The eggs are very large, and float in the water, where they may become surrounded by a swarm of spermatozoids so numerous that the egg is actually set in motion and begins to rotate. One spermatozoid finally enters the egg and fertilizes it. The fertilized egg, or zygote, develops directly into a new *Fucus* plant (Figs. 622, 623).

Alternation of generations in *Fucus*. The *Fucus* plant is diploid. Meiosis, or reduction in the number of chromosomes, takes place in the first two cell divisions of the antheridium and oogonium respectively.

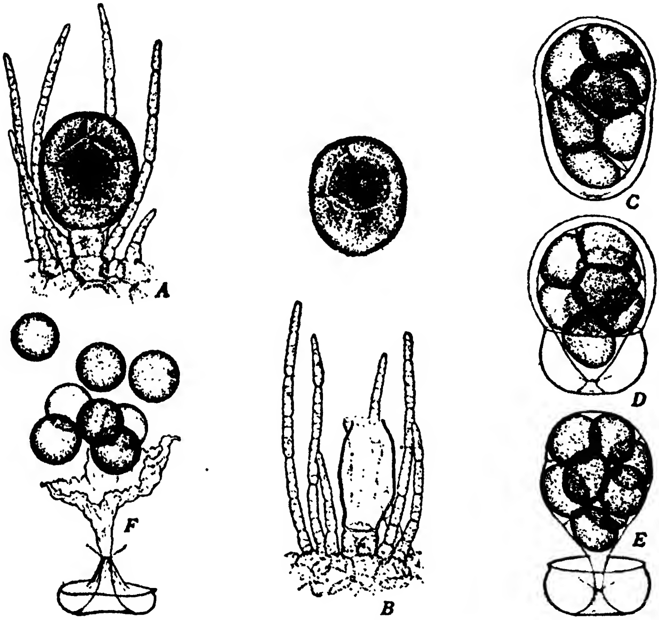


FIG. 621. *Fucus vesiculosus*

Escape of eggs from oogonium: *A*, single oogonium surrounded by sterile filaments; *B*, contents of the oogonium surrounded by two layers of the oogonium wall have escaped from the outer layer of the oogonium wall; *C*-*E*, escape of eggs surrounded by the inner layer of the oogonium wall from the middle layer of the oogonium wall; *F*, escape of eggs from inner layer of oogonium wall. (After Thuret)

Therefore at the four-nucleate stage of both antheridium and oogonium the nuclei are haploid. From this it follows that, beginning with the four-nucleate stage and continuing until the formation of spermatozoids and eggs, the nuclei of the antheridium and oogonium are haploid. The diploid condition is restored when the egg is fertilized by a spermatozoid.

In *Fucus* there is no alternation of two distinct and independent kinds of plants. For this reason some botanists say that in *Fucus* there is no alternation of generations. However, a diploid gametophyte is certainly exceptional, and we have noted that the gametophytes in the other groups of brown algae are haploid. Some authorities suggest that the *Fucus* plant may represent an asexual generation and the gametes a sexual one. In *Laminaria* the female gametophyte may consist of only a single cell the contents of which form an egg. It has been suggested that in *Fucus* the reduction of the gametophyte is more extreme and that the asexual spores have become modified and function directly as gametes. If we assume that there was a regular alternation of generations in the ancestry of *Fucus* it may be that there was a gradual reduction in the gametophyte, but such an assumption is not the only possible one. It has been pointed out that in *Ectocarpus* haploid zoospores formed in unilocular zoosporangia may, instead of producing sexual plants, function as gametes. It is possible that such a condition became permanent in some distant ancestor of *Fucus*. It should be remembered that these ideas as to alternation of generations in the ancestry of *Fucus* are based on analogy with other groups in the *Phaeophyta*. Such views as those mentioned above are therefore highly speculative, and the possibility is not excluded that the condition found in *Fucus* may have originated in some other way; for example, that the *Fucus* plant evolved from the diploid phase of a unicellular ancestor.

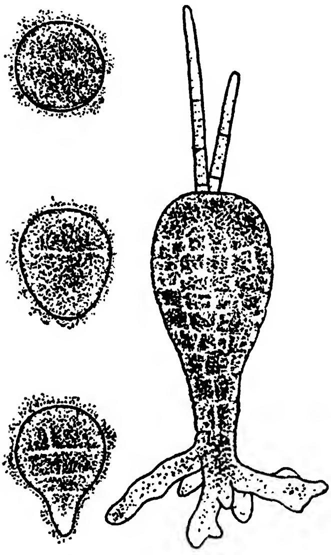


Fig. 622. Germination of egg of *Fucus vesiculosus*. (× 160)

(After Thuret)

RELATIONSHIP

The relationship of the *Phaeophyta* may be with the *Chrysophyta*, as is indicated by the facts that they have a brown color, that they do not produce starch, and that typically the reproductive cells have two unequal flagella, one of which projects forward and the other backward. In the *Phaeophyta*, however, the nature of the stored food and the insertion of the flagella are very distinctive, and the differences between all the *Phaeophyta* and all known members of the *Chrysophyta* are so great that the two groups are generally regarded as distinct. If there appear to be no very simple members in the *Phaeophyta*, this may be because such forms died out long ago. The absence makes it impossible to trace the known brown algae back to simple ancestors. However, the brown algae have in common sufficient distinctive characters to indicate that they all had a common ancestor. Prominent among these distinctive common characters are the structure of the motile cells, the pigmentation of the chromatophores, and the products of photosynthesis.

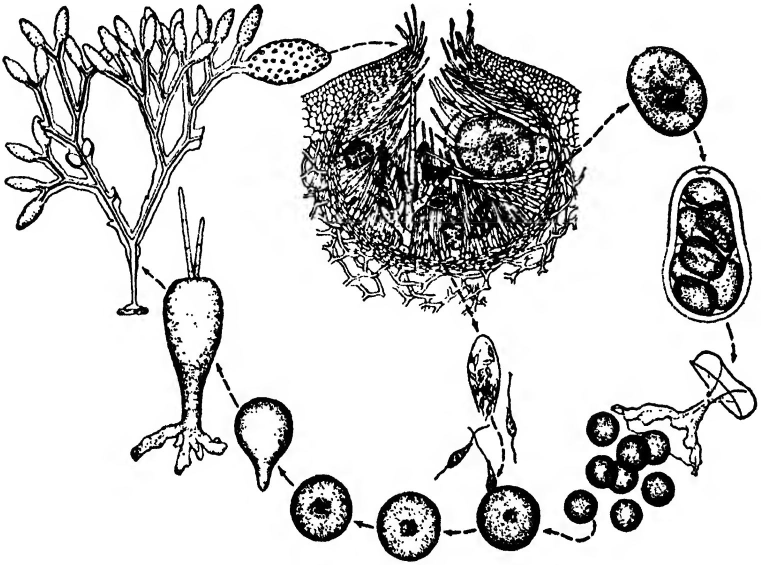


FIG. 623. Diagram of life history of *Fucus*

ECONOMIC USES

The economic importance of the brown algae is comparatively slight. Some of the kelps are rather extensively used as food in China and Japan. The ash obtained by burning kelps and *Fucus* is a source of iodine, and, as it is rich in potassium, has been used for producing this element when economic conditions permitted.

CHAPTER XXIII

RHODOPHYTA (RED ALGAE)

General characteristics. The red algae compose a very large group of small or medium-sized plants, and include the majority of seaweeds. They are predominantly marine; there are only a few fresh-water representatives. The red algae are frequently abundant along the coasts, and are often objects of great beauty. The name refers to the red or purple color which is characteristic of the great majority of the red algae. The color is due to a red pigment, phycoerythrin, which is usually present in such abundance as to mask the chlorophylls and carotinoids. Phycocyanin, the blue pigment so characteristic of the blue-green algae, has been found in many of the red algae. A close study may show that it is characteristic of the whole group. The pigments of the red algae occur in definite chromatophores. While the red color is very prominent in the red algae as a whole, there are many in which the red pigment is less prominent with the result that the plants are greenish, olive, or brown in color. This is true of the majority of fresh-water forms and of many marine forms growing in shallow waters. In such cases the general character of the plant body, and particularly of the reproductive organs, shows clearly that the individual belongs to the red algae.

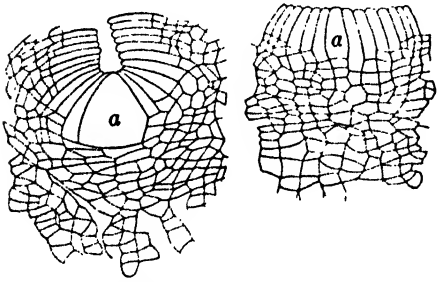


Fig. 624. Apical cell of *Fucus furcatus*

Left, section through apical cell made at right angles to the surface of the thallus; left, section made at right angles to preceding section. (× 125). After Woodworth

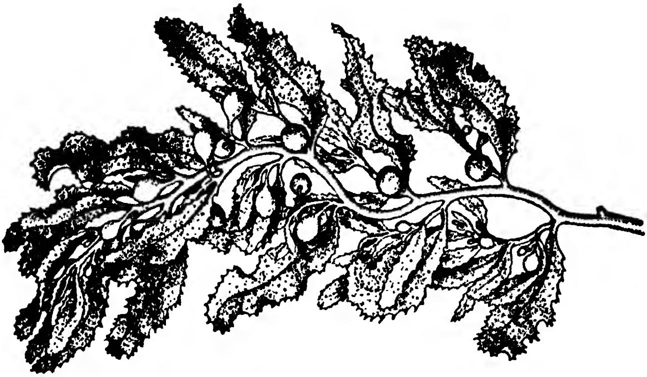


FIG. 625. *Sargassum*. (× ¾)

Note that the plant is divided into stemlike and leaflike portions and also has rounded air bladders which contain air and add to the buoyancy of the plant. *Sargassum* belongs to the *Fucales* and is closely related to *Fucus*

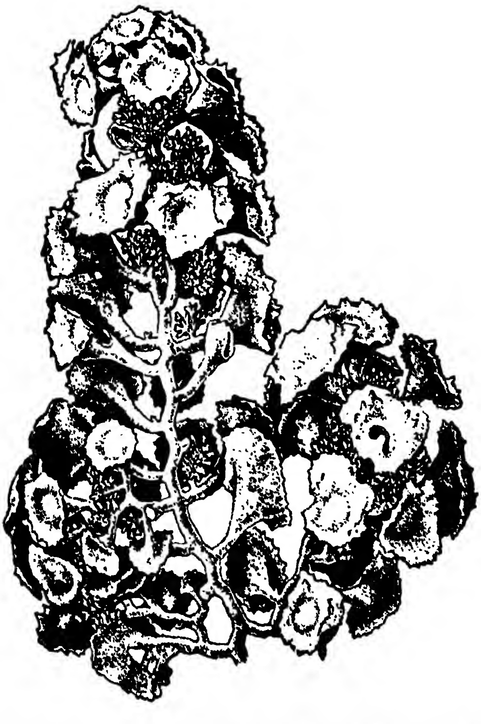


FIG. 626. ***Turbinaria*, one of the *Fucales* closely related to *Sargassum*.** (× ¾)

The variety in structure and appearance among the red algae is very great (Figs. 628, 629, 637). They are attached to the substratum by disklike holdfasts or special filaments. Often the plant consists of a mass of slender branched filaments (Fig. 628), in many species there are large and small branches (Fig. 629), while expanded thalli are also numerous (Fig. 628); these may be unbranched or may branch in a great variety of ways.

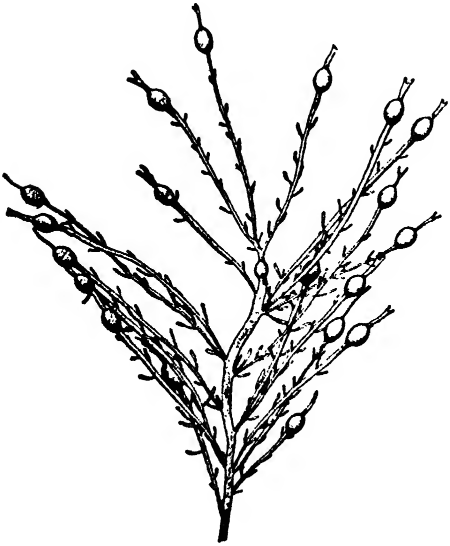


FIG. 627. *Ascophyllum nodosum*, one of the *Fucales* closely related to *Fucus*. (× ⅓)

An important characteristic of the red algae is that there are no flagellated reproductive cells. Sexual reproduction is never isogamous, but is always due to the fertilization of a large female cell by a small male cell. The nucleus of the red algae, except in the simpler forms, is highly developed, is bounded by a definite limiting nuclear membrane, and divides by the complicated process of mitosis (Fig. 630). Such nuclei are very much like those of higher plants in both structure and method of division.

Sexual reproduction. The reproductive organs of the red algae are so different from those of other algae that they have been given distinctive names. The female reproductive organ which corresponds more or less to the oogonium of the green algae is known as a procarp (Figs. 631, 632). In fairly simple forms the procarp has a swollen basal portion (known as a carpogonium) which contains the female nucleus, and a long slender projection, the trichogyne (Fig. 631). The antheridia are single-celled structures (Figs. 631, 636); in some cases the contents are discharged as non-motile male cells, in other cases the whole antheridium acts as the male cell.

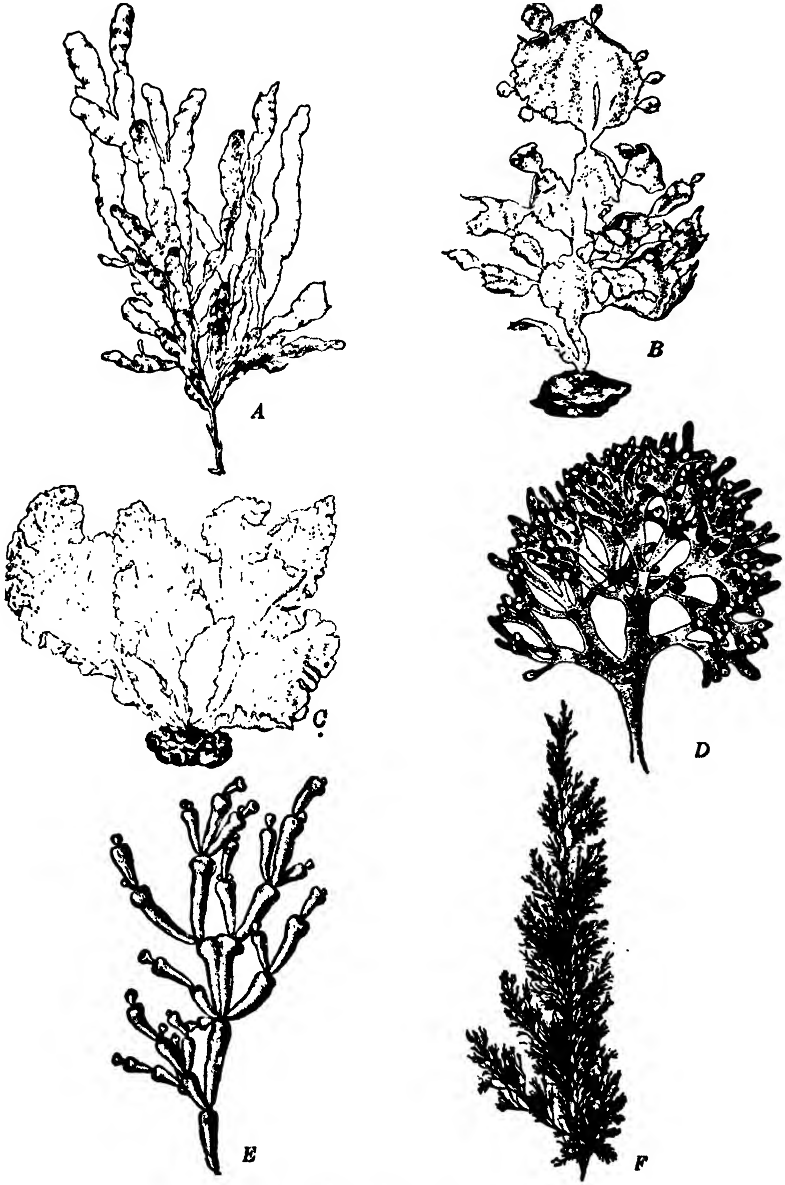


Fig. 628. Various forms of red algae

A, *Phyllophora clevelandia*; *B*, *Opuntiella californica*; *C*, *Grinnellia americana*; *D*, *Chondrus crispus*; *E*, *Corallopsis salicornia*; *F*, *Polysiphonia violacea*. (A–C, × about 1/3; D–F, × about 1/2)

When the male cells are discharged they are, in some cases, surrounded by cell walls. In others they have been reported as being naked, but as soon acquiring cell walls.

The male cells, having no motility of their own, are carried by the movement of the water, and it is by chance that they come in contact with the tips of the trichogynes (Figs. 631, 632, 636). When a male cell is caught on a trichogyne the cell walls between the two are dissolved, and the nucleus of the male cell enters the trichogyne, passes through it, and fuses with the female nucleus.

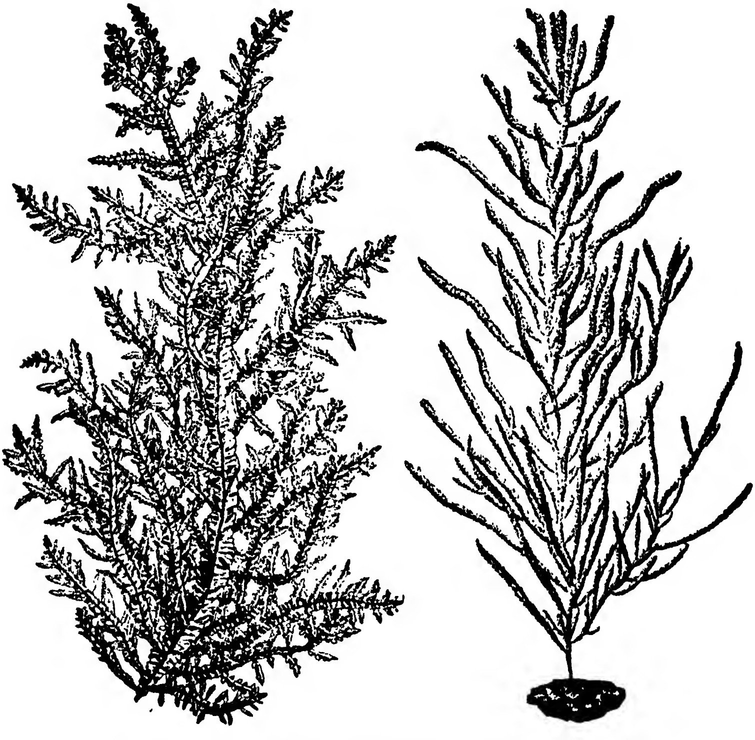


Fig. 629. Two beautiful branching forms of red algae
Left, *Dalesseria*; right, *Dasya elegans*

Carpospores. In the red algae the fertilized female cell does not germinate to produce a new plant, but further development ensues which results in the formation of asexual spores known as carpospores. Usually these are formed at the ends of branches which are outgrowths of the carpogonium (Figs. 631, 636) or of a larger mass formed by the fusion of neighboring cells (Figs. 638, 641). In any case the nucleus of the carpospore is a descendant of the fertilized female nucleus.

Alternation of generations. In the simpler red algae the carpospores, on germination, produce sexual plants (Figs. 631, 634). In the majority of red algae, however, the carpospores give rise to asexual plants which bear tetraspores. The tetraspores get their name from the fact that four of them are borne in a tetrasporangium (Fig. 632). The tetraspores, on germination, produce sexual plants. In the great majority of red algae there is, then, an alternation of an asexual generation con-

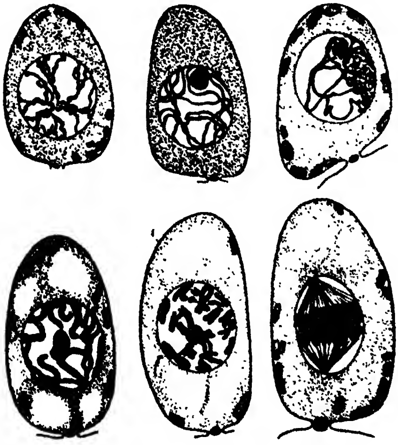


Fig. 630. First meiotic division in *Polysiphonia violacea*

After Yamanouchi

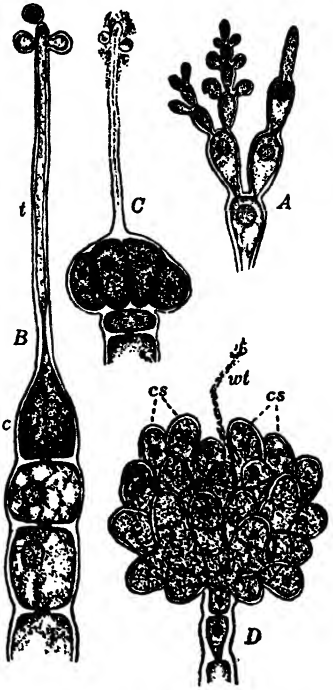


Fig. 631. *Nemalion multifidum*

A, antheridia, consisting of groups of small cells, each of which develops a single male cell; the vegetative branch at the right illustrates the method of terminal growth and the protoplasmic connections between the cells. *B*, the female cell, or carpogonium, *c*, with its trichogyne, *t*, to which are attached three male cells. *C*, early stage in the development of the cystocarp; the trichogyne above has begun to wither. *D*, mature cystocarp composed of fertile filaments which develop the carpospores, *cs*, terminally; *wt*, withered trichogyne

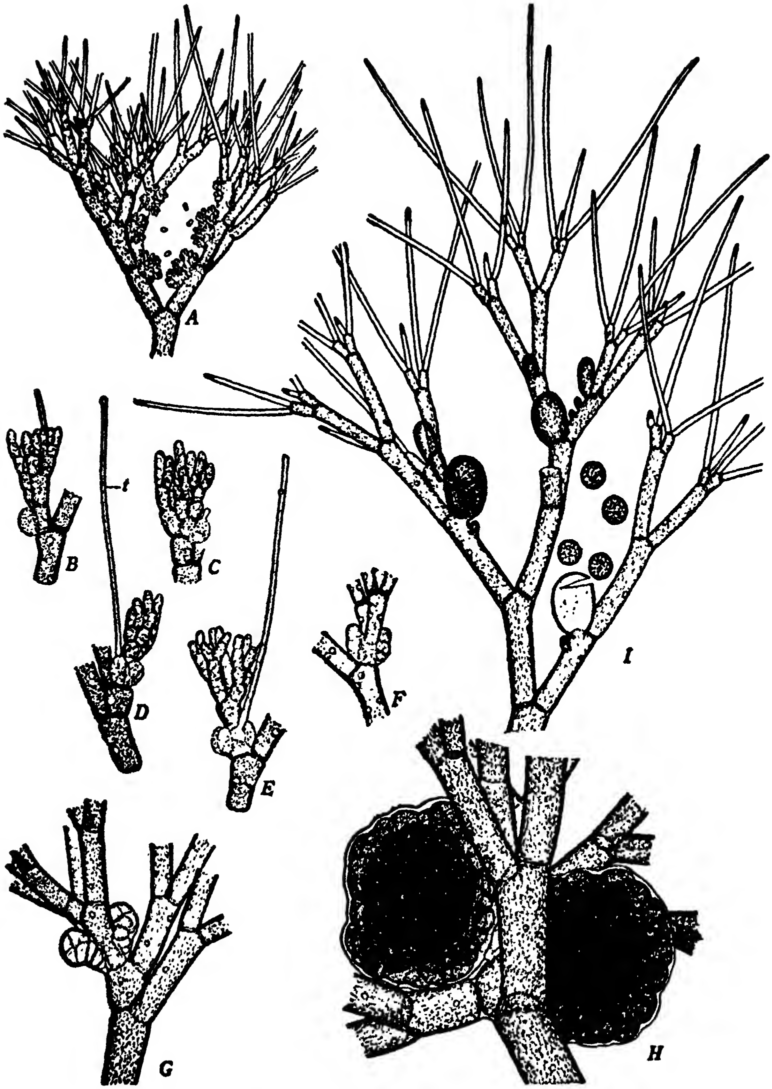


Fig. 632. *Callithamnion corymbosum*

A, portion of a plant with antheridia; *B*, a small branch showing the beginning of the development of a procarp on the left; *C*, somewhat old stage of procarp development; *D*, the procarp consisting of several cells is mature and has a long trichogyne, *t*; *E*, a male cell is seen united to the trichogyne; *F*, *G*, early stages in carpospore formation; *H*, mature carpospores; *I*, portion of tetrasporic plant with tetrasporangia in various stages of development, four tetraspores escaping from a ripe tetrasporangium. (After Thuret) sisting of a tetrasporic plant and a sexual generation consisting of male plants and female plants (Figs. 632, 633). In such cases the fertilization of the female cell, or carpogonium, results in the production of carpospores, which, on germination, give rise to tetrasporic plants.

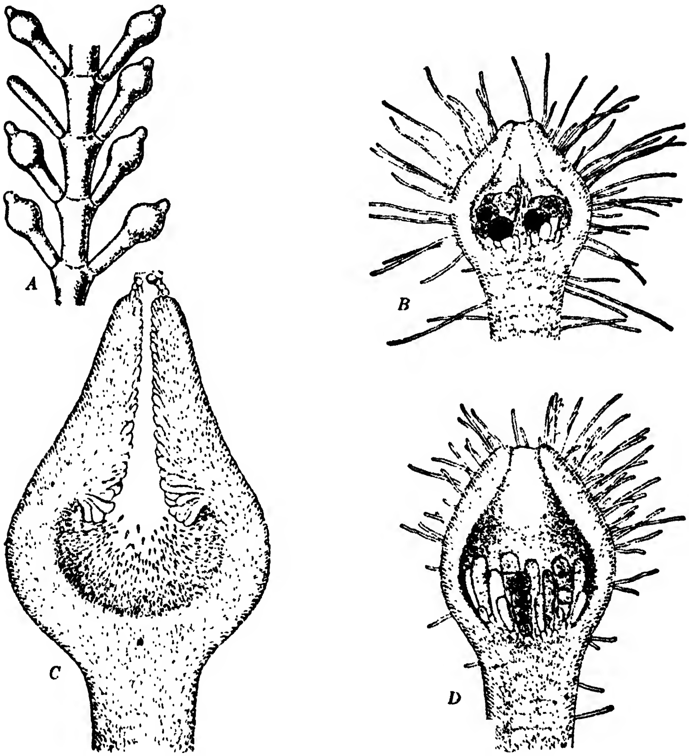


FIG. 633. *Corallina mediterranea*

A, portion of a branch with antheridial conceptacles; *B*, section showing carpospores; *C*, section of antheridial conceptacle showing antheridia; *D*, section showing tetraspores. (After Thuret)

NEMALION

Reproduction. The genus *Nemalion* may be taken as an example of one type of red algae. The plant body consists essentially of branched filaments (Fig. 631). The antheridia are single-celled structures which are borne in clusters at the ends of short branches. The male cell, which contains two nuclei, is discharged from the antheridium. The procarp consists of two parts: a swollen portion, the carpogonium, which contains the female nucleus, and a long slender structure, the trichogyne, which projects from the carpogonium and which contains a nucleus that degenerates. One or more male cells may come in contact with the trichogyne. The walls separating the contents of the trichogyne and a male cell are dissolved, and the contents of the male cell pass into the trichogyne. One of the nuclei of the male cell then moves down through the trichogyne and fuses with the female nucleus, thus fertilizing the carpogonium. Short branches then grow up from the carpogonium, and an asexual spore, known as a carpospore, is formed at the tip of each of these branches. When a carpospore germinates, it produces a new *Nemalion* plant. The carpogonium plus the filaments and carpospores is known as a cystocarp.

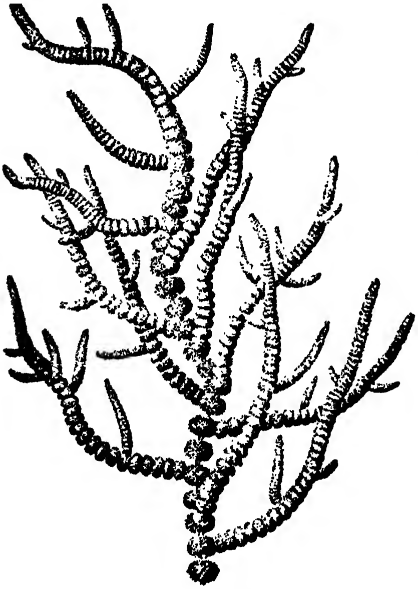


FIG. 634. *Batrachospermum*

Habit of portion of plant. (× 5)

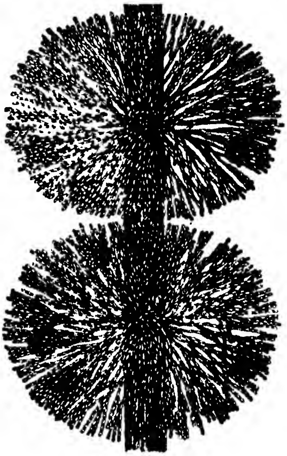


FIG. 635. *Batrachospermum* showing whorls of branches

The dense rounded masses of cells near the periphery of the whorls are cystocarps. (×45)

The *Nemalion* plant is haploid. The nucleus of the fertilized carpogonium is diploid. Reduction in the number of chromosomes takes place in the first two divisions of the carpogonium nucleus; so the branches which give rise to carpospores, and the carpospores themselves, are haploid. In *Nemalion*, therefore, there is an alternation of a plant producing sexual organs and a stage which results in the formation of asexual carpospores, but there is no alternation of diploid and haploid plants.

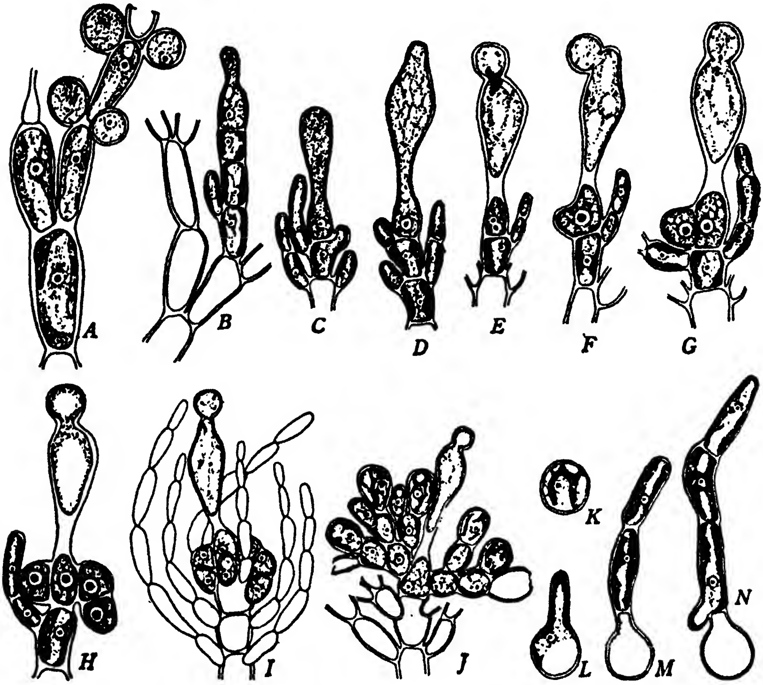


FIG. 636. *Batrachospermum moniliforme*

A, antheridial branch with rounded antheridia. *B*, early stage in development of carpogonium; the uppermost cell is the carpogonium, at the tip of which the trichogyne is developing. *C*, *D*, later stages in the development of carpogonium and trichogyne. *E*, male cell has fused with trichogyne and male nucleus is fusing with the carpogonium nucleus. *F*, the male and carpogonium nuclei have fused. *G*, the carpogonium is beginning to send out a branch; below on either side are sterile branches which will form part of the covering of the cystocarp. *H*, a second branch is growing from the carpogonium. *I*, further stage in branching of carpogonium; the sterile covering of the cystocarp is much further developed. *J*, carpospores. *K*, a single carpospore. *L*–*N*, germination of carpospore. (After Kylin)

Batrachospermum. *Batrachospermum* is a rather common red alga living in fresh waters. In *Batrachospermum* there are large branches which are cylindrical and from which grow whorls of branching filaments (Figs. 634, 635). The life history is similar to that of *Nemalion* (Fig. 636), but the cystocarp is more like that of most red algae (Fig. 637) in that sterile filaments grow from cells near the carpogonium and form a covering around the carpospores (Figs. 635, 636).

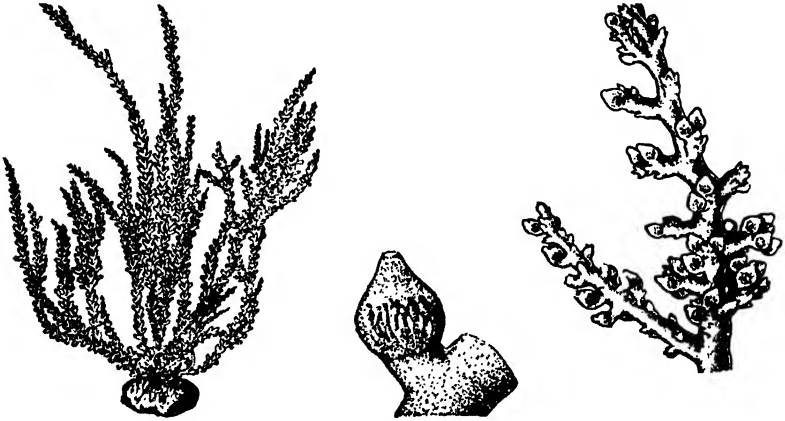


FIG. 637. *Acanthosporea therii*

Left, habit (× ½); right, branch of a female plant with many cystocarps (× 4); center, a cystocarp with carpospores. (× 16)

POLYSIPHONIA

General characteristics. *Polysiphonia* is a very common marine alga, and is a classic example of the complicated type of alternation of generations found in the red algae. The thallus consists of branched multicellular filaments (Fig. 628). As in many red algae, there is a central row of cells, known as the central siphon, which is surrounded by peripheral cells formed from it. Between the cells there are the prominent protoplasmic connections which are so characteristic of the red algae.

Sexual reproduction and cystocarp formation. In *Polysiphonia* there is an alternation of an asexual generation producing asexual tetraspores and a sexual generation consisting of male plants and female plants. There are thus three types of *Polysiphonia* plants. These are plants with tetraspores, plants with antheridia, and plants with cystocarps. These three kinds are so much alike that they cannot be distinguished by the naked eye. The antheridia are small single-celled structures, and are borne in large numbers on antheridial branches (Fig. 638). The procarp of *Polysiphonia* and the method in which cystocarps are produced are more complicated than in *Nemalion* (Fig. 631). As in other red algae showing an alternation of generations, the procarp consists of several cells. As in *Nemalion* and most red algae, there is a carpogonium with its nucleus, and projecting from it a trichogyne with its nucleus. As is usual in red algae, a male cell comes in contact with the trichogyne; the walls between the two are dissolved; and the male nucleus migrates through the trichogyne and fertilizes the female nucleus in the carpogonium. The branches which give rise to carpospores do not grow from the carpogonium itself but from a

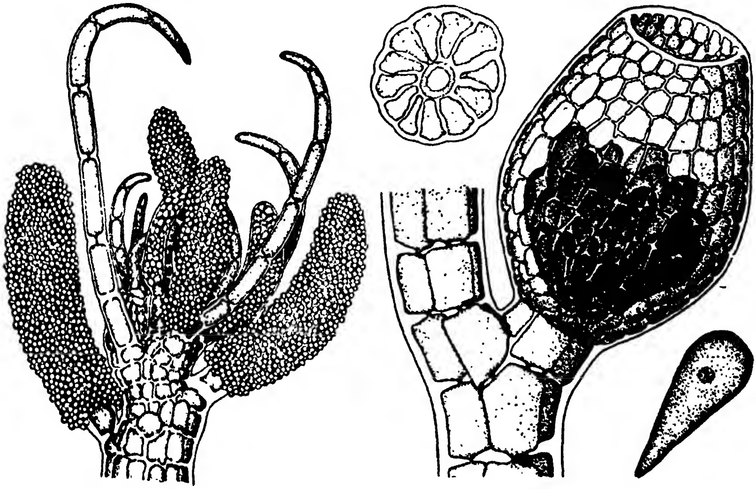


FIG. 638. *Polysiphonia*

Left, a branch of a male plant with large club-shaped antheridial branches; center, section of vegetative portion of thallus; right, branch of female plant with cystocarp containing carpospores; lower right, a single carpospore much larger aggregate which is formed by the fusion of neighboring cells and is supplied with nuclei derived from the fertilized female nucleus. While the carpospores are being formed, the characteristic urn-shaped envelope of the cystocarp is produced from the peripheral cells of the branch which gave rise to the cystocarp.

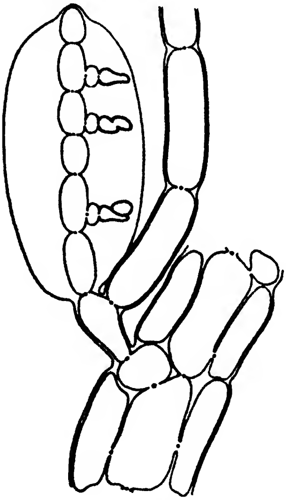


Fig. 639. Diagram of antheridial branch of *Polysiphonia*

Note successive stages in cutting off of antheridium which functions as a male cell. (After Yamanouchi)

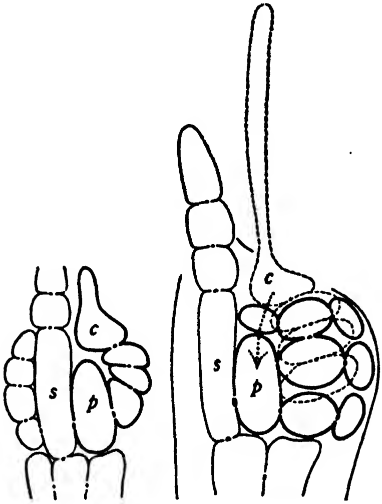


Fig. 640. Diagram of carpogonium of *Polysiphonia*

s, cell of central siphon; *p*, pericentral cell; *c*, carpogonium from which trichogyne is developing. Right, an older stage. The cells of the carpogonial branch are shown in dotted lines. Numerous auxiliary cells have developed from the pericentral cell and one is between the pericentral cell and the carpogonium. The arrow shows the direction in which the nuclei migrate from the carpogonium to the pericentral cell. (Modified after Yamanouchi)

Antheridia of *Polysiphonia*. An antheridial branch consists of an axial row of cells or axial siphon, from which grow numerous lateral branches. A lateral branch consists of a stalk cell and an antheridium mother cell. From the antheridium mother cell there is constricted off a single-celled antheridium (Fig. 639). The antheridium, without undergoing any change, functions directly as a male cell. The contents do not escape but remain within the wall of the antheridium, which thus serves as a wall for the male cell. After the separation of the first antheridium, others are successively constricted off from the mother cell in the same manner.

Procarp of *Polysiphonia*. The first stage in the formation of the procarp is that the central siphon gives rise to a large lateral cell, the pericentral cell (Fig. 640). From the pericentral cell there grows out a carpogonial branch consisting of four cells, the apical one of which forms the carpogonium with its trichogyne. The nucleus of this cell divides into two, one of which remains in the base of the carpogonium and functions as an "egg," or carpogonium nucleus, while the other moves into the trichogyne and ultimately disintegrates.

Fertilization and carpospore formation. By the time that the male nucleus has fused with the "egg," or carpogonium nucleus, the pericentral cell has given rise to a number of cells known as auxiliary cells. One of these lies between the carpogonium and the pericentral cell and becomes connected with both of these cells. The fertilized nucleus of the carpogonium has by now divided into two, both of which migrate from the carpogonium through the auxiliary cell just mentioned into the pericentral cell (Fig. 640). The carpogonium and its stalk cells finally disintegrate. The pericentral cell becomes fused with the auxiliary cells and finally with the cell of the central siphon. The original nuclei of the pericentral and auxiliary cells disintegrate, the fusion mass being supplied with nuclei derived from the division of the fertilized carpogonium nucleus. From the fusion mass there grow out lobes, the ends of which are constricted off as carpospores (Fig. 641). In this way sixty or more carpospores are produced.

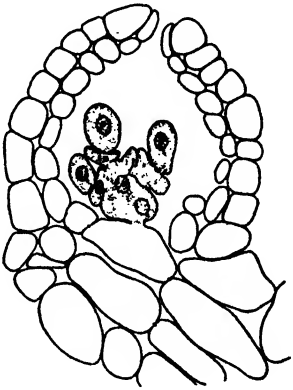


FIG. 641. *Polysiphonia violacea*

Section of cystocarp showing formation of carpospores. (After Yamanouchi)

Asexual reproduction and alternation of generations. The carpospores are asexual spores. When these germinate and produce new plants, these new plants are also asexual and produce asexual tetraspores. The tetrasporangium containing the four tetraspores is a rounded structure attached by a stalk cell to the central siphon. The tetrasporangium, therefore, is between the central siphon and the peripheral cells, and is thus inside the filament itself (Fig. 642). The tetraspores give rise to the sexual generation consisting of male plants and female plants.

In the life history of *Polysiphonia*, therefore, we do not have simply an alternation of a sexual and an asexual generation. Sexual reproduction results in the formation of carpospores, which give rise to asexual tetrasporic plants, and these in turn to sexual plants. Between the sexual generation and the asexual tetrasporic generation there is therefore another asexual phase in which asexual carpospores are produced.

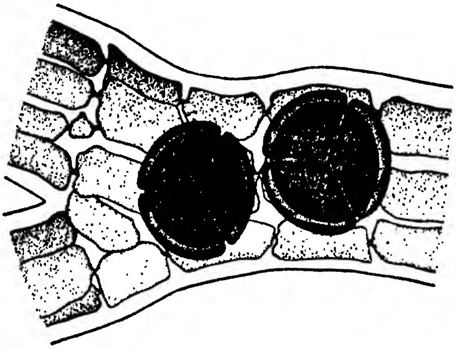


FIG. 642. *Polysiphonia violacea*
Branch of tetrasporic plants containing tetraspores

The tetrasporic plants of *Polysiphonia* are diploid. The number of chromosomes is reduced during the formation of tetraspores, so that the tetraspores are haploid, as are the gametophytic plants which they produce. When the carpogonium nucleus is fertilized the diploid condition is restored. This condition persists throughout the stages leading to carpospore formation, so that the carpospores are diploid, and these, on germination, produce the diploid tetrasporic plants. The diploid condition is thus not confined to the tetrasporic plants but is also found in the stages from fertilization to carpospore formation. The result is that there are two diploid phases, one consisting of stages leading to carpospore formation, while the other is the tetrasporic plant. *Polysiphonia* thus differs from *Nemalion* not only in having an alternation of gametophytic and sporophytic plants but also because the stages in carpospore formation are haploid in *Nemalion* and diploid in *Polysiphonia*.

BANGIALES, THE SIMPLER RED ALGAE

General characteristics. The great majority of the red algae are complicated structures such as we have considered. There are, however, some with a much simpler organization which are placed in the order *Bangiales*. Two of the best-known genera of the *Bangiales* are *Bangia*, in which the plants are unbranched filaments (Fig. 643), and *Porphyra*, in which the plant is a delicate sheet one cell in thickness (Fig. 644). The simplest of the *Bangiales* and of all the red algae is *Porphyridium*, in which the plant consists of a single cell (Fig. 645). The cells of the above-mentioned plants are characterized by having a single large stellate chromatophore, in the center of which is a colorless body, the pyrenoid. There is a single nucleus, which in a resting condition appears to be dense and homogeneous and resembles a nucleolus. The division of the nucleus is not like that in higher plants, but appears to be somewhat intermediate between mitotic division and amitosis. In fact, the process of nuclear division, particularly that in *Porphyra*, has been described as showing much similarity to the division of the central body in certain of the blue-green algae.

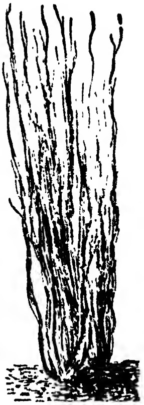


FIG. 643. *Bangia vermicularis.* (× ½)

Reproduction. The reproduction in *Porphyra* may be taken as an example of reproduction in the *Bangiales* (Fig. 644). In *Porphyra* all of the plants have the same general appearance, but there are two kinds, male and female. The female plants produce carpogonia, which are, however, only slightly modified vegetative cells. The modification consists primarily in a small projection or papilla which may be regarded as a rudimentary trichogyne. The antheridia occur in the male plants. They are produced from vegetative cells, the contents of which divide up to produce a considerable number of male cells. The male cell is carried by the water to the trichogyne as in other red algae. The nucleus of the male cell enters the trichogyne, passes in, and fuses with the nucleus of the carpogonium. The contents of the carpogonium then divide up to form a number of carpospores. The sexual organs in this case are certainly much simpler than those in most of the red algae, and are generally regarded as more primitive.

Porphyridium. The *Porphyridium* plant is, as mentioned above, composed of a single cell (Fig. 645). The only known method of reproduction is by the division of a cell into two. Sexual reproduction is unknown. *Porphyridium* is a terrestrial alga, growing on damp soil and walls. It is

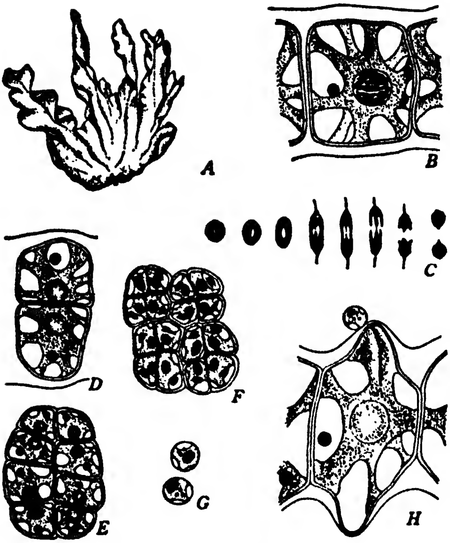


FIG. 644. *Porphyra*

A, habit of plant. *B*, section of the thallus, which is a single cell in thickness; in the section are shown a single cell and parts of two neighboring cells; the branching structure which appears to occupy most of the cell is a chromatophore, in the center of which is a large pyrenoid; the black dot to the left is a nucleus. *C*, stages in division of nucleus. *D*, *E*, *F*, division of cells to form antheridia. *G*, male cell. *H*, carpogonium with male cell in contact with trichogyne. (All except habit after Ishikawa)

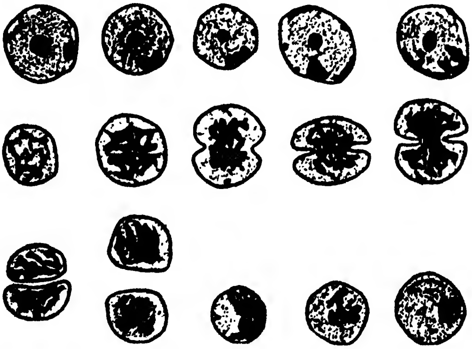


FIG. 645. *Porphyridium cruentum*

Upper left drawing shows structure of a resting cell. Most of the cell appears to be occupied by the chromatophore. The large black spot in the center of the chromatophore is the pyrenoid. The black spot to the right and near the wall is the nucleus. The following drawings illustrate stages in division and reconstruction of the nucleus. (After Lewis and Zirkle) certainly the simplest of the known red algae. It is, however, such an isolated form that it is difficult to establish its position. It is not easy to tell whether its simplicity is due to its being a primitive form or whether it is a reduced form and its simplicity is an adaptation to a terrestrial habitat as in the case of *Protococcus* among the green algae.

RELATIONSHIP OF RED ALGAE

The red algae are so distinct from other algae that their origin and relationships have long been considered as obscure and questionable. Their red color, lack of motile cells, and specialized sexual reproduction mark them off sharply from those groups of algae which can be traced back to a flagellate origin. They form, therefore, a distinct series. It is interesting that in some of the blue-green algae we find phycoerythrin, the red pigment which is so characteristic of the red algae; also that many of the red algae contain phycocyanin, the blue pigment of the blue-green algae. Another point of similarity between blue-green and red algae is that both groups lack flagellated cells.

The similarity in pigments in the blue-green and red algae, the lack of flagellated cells in both groups, and the simple character of the nucleus of the simpler red algae suggest a possible relationship between the red and the blue-green algae. Such a relationship would explain the lack of motile cells in the red algae. It would also explain the occurrence in the red algae of the red pigment phycoerythrin and the related blue pigment phycocyanin, which are found in the blue-green algae.

To one who has not learned the exactness demanded by science it might seem logical to think of *Porphyridium* as a primitive red alga descended from a blue-green ancestor. The more complicated members of the *Bangiales*, such as *Porphyra*, might then be thought of as being derived from such forms as *Porphyridium*, and the higher red algae in turn from the *Bangiales*. However, it should be remembered that it is very hard to tell whether the simpleness of *Porphyridium* is due to its being primitive or whether it is a reduced form.

The red algae are sharply marked off from the blue-greens by the presence of definite chromatophores and their highly differentiated sexual reproduction. While there may be some relationship between the blue-green and the red algae, this relationship can hardly be close.

CHAPTER XXIV

MYXOMYCETES (SLIME MOLDS)

General characteristics. We have seen that the flagellates combine animal and plant characteristics. The *Myxomycetes* are another relatively simple group which show a combination of features found in plants with others which are more characteristic of animals. Owing to these facts there has been considerable disagreement as to their place among living things. Many authorities believe that they should be considered as plants, while others maintain that they belong in the animal kingdom. The *Myxomycetes* lack photosynthetic pigments; therefore they must, like animals, obtain their food in organic form. During their vegetative development they consist of naked protoplasm and are very much like animals not only in nutrition but also in structure and movement. They form fruit bodies with plantlike features, however, including spores with cellulose walls. It appears that they have developed from flagellates, perhaps flagellates which lacked plastids; that they have retained the animal-like characteristics of their flagellate ancestors; and that, like other plants which have developed from flagellates, they have acquired plant characteristics.

Sporangium. The fruit body of *Stemonitis,* a common and widely distributed form, will serve as a convenient starting point for the discussion of the group (Fig. 646). The fruit bodies often grow together in clumps of considerable numbers. An individual fruit body consists of an elongated terminal sporangium with a slender stalk. The stalk continues into the sporangium as a column, known as a columella. The sporangium is covered by a firm membrane, the peridium. Around the columella and springing from it is a network of threads, the capillitium; and tangled in the capillitium are very numerous spores (Fig. 647). The peridium of

Stemonitis is thin, and breaks to pieces when the sporangium is mature. The capillitium is hygroscopic, and the spores are scattered by its movement and the action of the wind.

The sporangia of the *Myxomycetes* are usually very small, and there is considerable variety among them (Figs. 646–649). Some have stalks, others do not. In many the individual sporangia are separate, in others they coalesce to a greater or less extent. Usually there is one sporangium to a stalk, but there may be more. In many genera there is no columella.

Life history. The spores of the *Myxomycetes* remain inactive as long as they are dry. When placed under proper conditions, including sufficient moisture, they germinate (Fig. 650). The contents swell; the spore wall is ruptured; and (usually) a single protoplast emerges. This soon becomes pear-shaped and develops a single flagellum at the anterior end. During this stage it is known as a swarmspore. The swarmspore may move by means of its flagellum or by amoeboid movements. After a time it loses its flagellum and comes to be like an amoeba It is then known as a myxamoeba. The myxamoeba is irregular

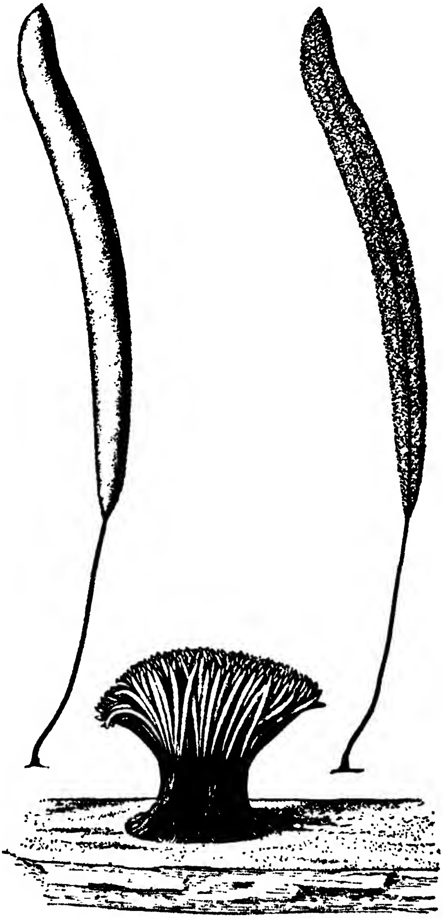


Fig. 646. *Stemonitis*

Center, group of sporangia; left, single sporangium with peridium intact; right, capillitium after disappearance of peridium in shape, and moves about, as do amoebae, by sending out protoplasmic processes and crawling by movement of the protoplasm. Both the swarmspore stage and the myxamoeba stage increase in numbers by division of one individual into two. They ingest solid particles, including bacteria. The bacteria are surrounded by vacuoles which do not contract, and in these they are digested.

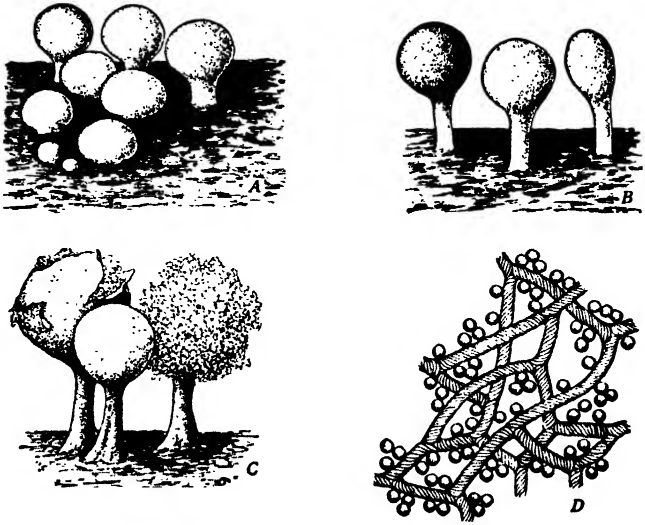
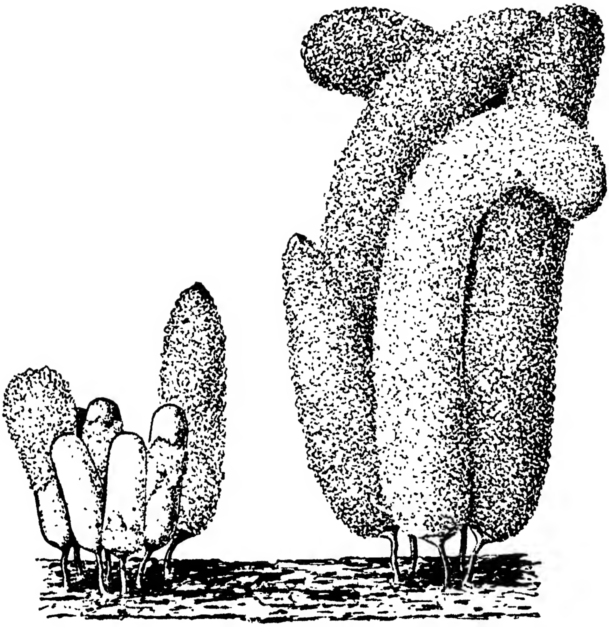


Fig. 647. *Hemitrichia*

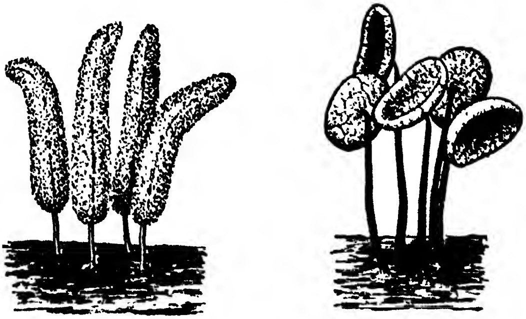
A and *B*, stages in development; *C*, a mature sporangium unopened, with peridium intact, another with capillitium showing, with peridium broken, and another after disappearance of peridium; *D*, threads of capillitium and spores. (*A*, *B*, *C*, × 15; *D*, × 250)

After a time division ceases and the myxamoebae come together and fuse in pairs (Fig. 650), the fusion of the protoplasm being followed by a fusion of the nuclei. These amoebozygotes do not enter on a resting stage, but continue active and come together and unite in considerable numbers. The nuclei, which are now diploid, do not fuse further but divide repeatedly, giving rise to large numbers of nuclei. In this way there may be produced a considerable mass of naked protoplasm (Fig. 651) with various colors, often yellowish or brownish, and with a consistency not unlike that of the white of an egg. There are no cell walls, and the numerous



Fɪɢ. 648. *Arcyria*

In the group to the left are a specimen with a peridium intact, others in which the peridium is breaking, and one from which the peridium has disappeared except for the cup at the base. The group to the right shows the extent to which the capillitium expands after the disappearance of the peridium. (× 15)



Fɪɢ. 649. Two *Myxomycetes*

Left, *Comatricha* (× 20); note columella. Right, *Trichamphora* (× 10)

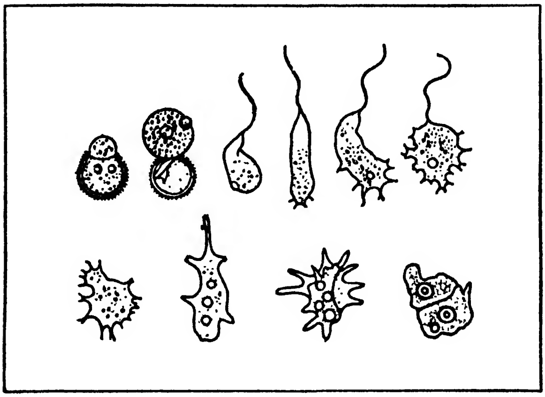


Fig. 650. **Germination of the spore and development of amoeba in a myxomycete, *Trichia varia***

Above, the germination of a spore, swarmspores, and transition to myxamoeba; below, myxamoeba and the fusion of two myxamoebae. (After De Bary and Cienkowski)

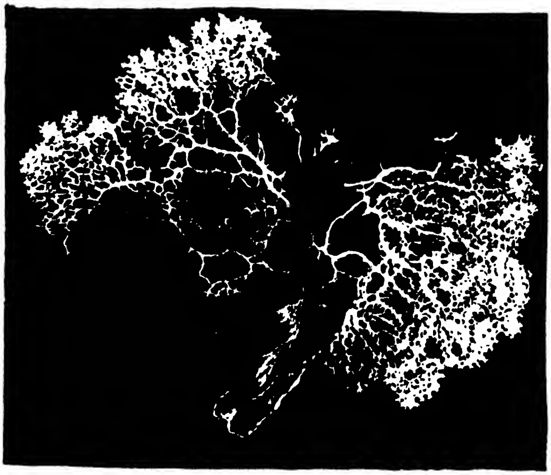


Fig. 651. **Plasmodium of *Didymium serpula*.** **(× 1)**

After Cienkowski

nuclei are distributed in the protoplasm. This mass is known as a plasmodium. It has no definite form, but may creep or stream about, and in doing so may take on very varied shapes. The plasmodium is like a giant or compound amoeba. It is owing to the slimy appearance of the plasmodium that the *Myxomycetes* are called slime molds. The plasmodium may increase in size by coalescing with other plasmodia or ingesting myxamoebae, or it may divide into two or more plasmodia by fragmentation. In moving about it takes in solid particles, such as bacteria and various kinds of debris, including small pieces of bark and leaves. A few ingest living fungi. The food material is digested and waste material left behind as the plasmodium moves on its way. The plasmodia are found in moist places, as in damp woods, around rotten logs, and on decaying leaves. The life history of a myxomycete, from the swarmspores to the formation and development of the plasmodium, shows very little resemblance to that of ordinary plants and is very animal-like in character.

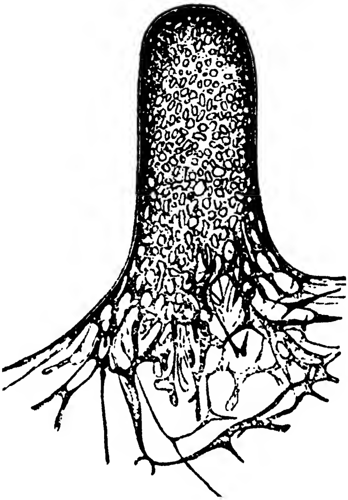


Fig. 652. An early stage in the formation of the sporangium of a myxomycete, *Ceratium hydnoides*, from the plasmodium

After De Bary

When the plasmodium is ready to form sporangia, its reactions to external conditions change and it creeps up into a lighter and drier place which is better suited to the scattering of the spores. Projections or papillae arise over the surface of the plasmodium, and these grow up to form the sporangia (Figs. 647, 652). In *Stemonitis* the stalk and its extension the columella are secreted in a canal in the center of the protoplasmic mass, and the protoplasm then climbs up over them to form the sporangium. The threads of the capillitium are formed in much the same way as the stalk and columella, and are secreted in a system of vacuole-like canals (Fig. 653). In some

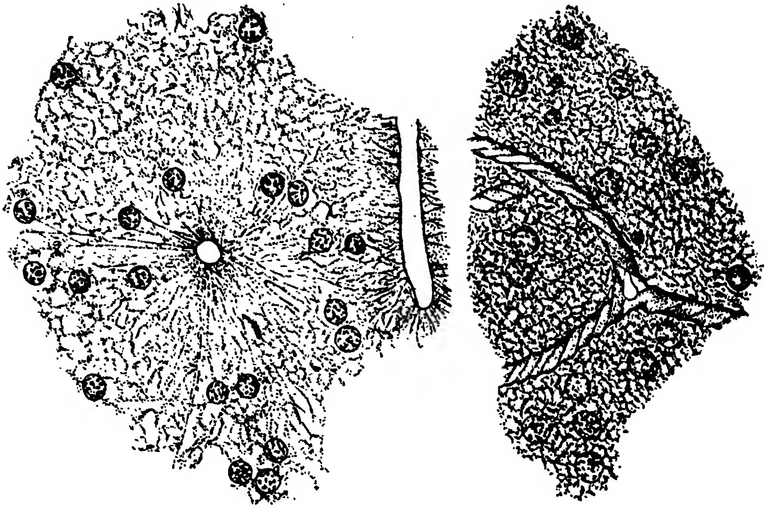


Fig. 653. Section of developing sporangium of a myxomycete, *Hemiarcyria clavata*

In the section on the left are seen numerous nuclei and a cross and a longitudinal section of canals at an early stage of capillitium formation. The section to the right shows the capillitium formed in the canals. (After Harper and Dodge)

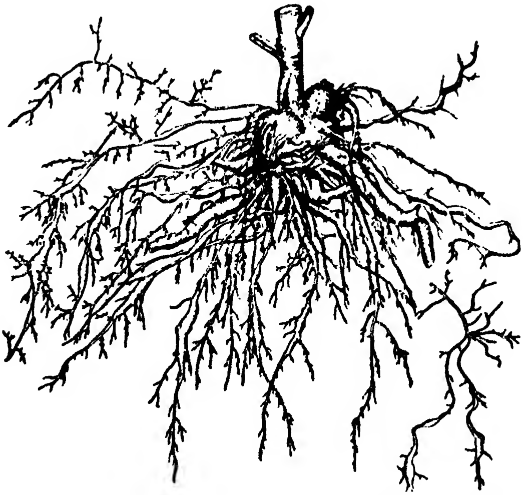


Fig. 654. Cauliflower root enlarged owing to infection by *Plasmodiophora brassicae*

After Woronin

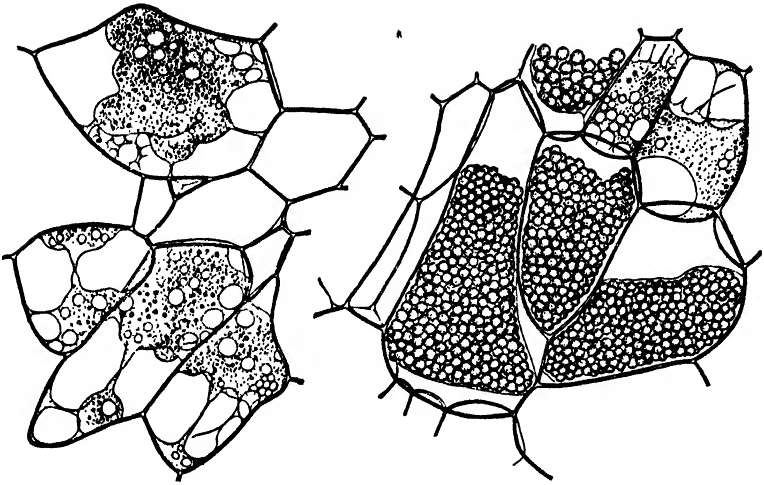


Fig. 655. *Plasmodiophora brassicae* in root cells

To the left is seen the plasmodium; to the right the plasmodium has given rise to spores. (× 360). After Woronin

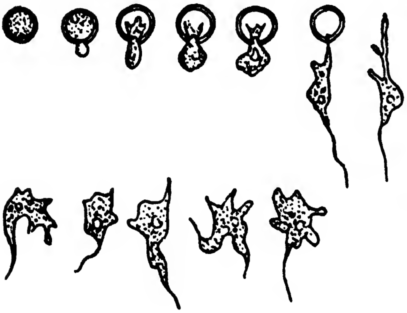


Fig. 656. Germination of spores of *Plasmodiophora brassicae* to form swarm-spores. (× 930)

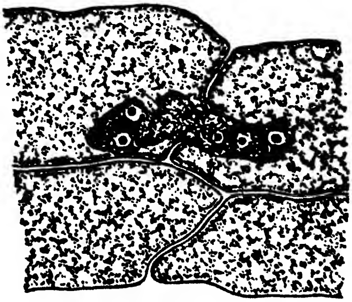


Fig. 657. *Plasmodiophora brassicae* passing through the end of a cell in the region of the cambium

After Kunkel

species of *Myxomycetes* with stalks, the stalk is a tube through which the plasmodium moves upward.

Prior to spore formation the nuclei divide and the chromosomes are reduced to the haploid number. At about the same time the protoplasm divides up by cleavage into smaller units. Finally each piece of protoplasm contains a single nucleus. Each protoplast then secretes a cell wall and becomes a spore. The sporangia of the *Myxomycetes* show some superficial resemblance to plant structures,

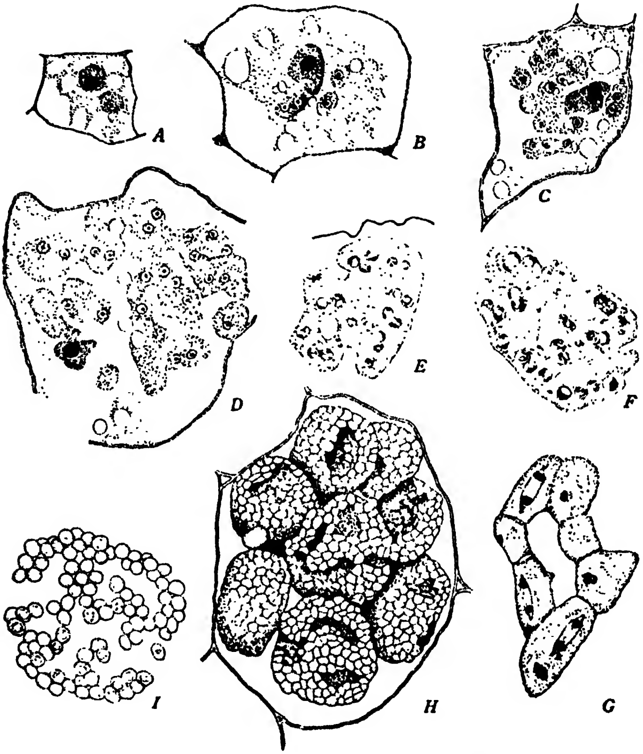


Fig. 658. ***Spongospora subterranea*, the causal organism of powdery scab of potatoes**

A, a single uninucleate amoeba in young host cell; *B*, three amoebae in a cell, one of which is binucleate; *C*, several small amoebae in a cell; *D*, formation of plasmodium; *E*, *F*, approaching and fusion of nuclei in pairs; *G*, anaphase of the second meiotic division; *H*, balls of spores in a host cell; *I*, section of spore ball showing spores. (After Osborn) but the method of their formation and the details of their structure are very different from those found in other plants. However, their general make-up is usually considered to be more like that of plants than that of animals.

Plasmodiophoraceae. There are a number of parasitic forms which appear to be rather closely related to the *Myxomycetes*. They are sometimes included in the *Myxomycetes*, but are more usually placed by specialists among the fungi, chiefly because they are parasites. Prominent among these are the *Plasmodiophoraceae*. Some of these cause serious plant diseases (Fig. 654).

The spores are formed in the cells of the host plant rather than in sporangia (Fig. 655). A spore germinates to produce a swarmspore as in the *Myxomycetes* (Fig. 656). The swarmspores enter cells of a host and become distributed in these cells as amoebae (Fig. 655). The amoebae become distributed in an increasingly large number of cells of the hosts by migrating through the cell walls (Fig. 657) and also by the divisions of the host cells themselves. After a time the amoebae in a cell unite to form a plasmodium which divides up to form spores (Fig. 658). Among the best-known of the *Plasmodiophoraceae* is *Plasmodiophora brassicae*, which causes clubroot of cabbage and similar plants (Fig. 654).

CHAPTER XXV

FUNGI (*PHYCOPHYTA*)

General characteristics. The fungi are a very large and diversified group of plants. Among the more familiar forms are molds and mushrooms. In general organization the fungi are in many respects like the algae. They differ from the algae, however, in that they lack chlorophyll and other photosynthetic pigments and so, instead of manufacturing their own food, are saprophytes or parasites. They are frequently colorless, but may have a great variety of colors and may even be green. The plant body may be very simple and may even consist of a single cell; however, in all except a comparatively small number which can be seen only under the microscope the plant body is composed of branching filaments known as *hyphae* (singular *hypha*). The hyphae form a tangled mass, called a *mycelium*. The hyphae are either rows of single cells or coenocytic threads. The mycelium may be a loose cobwebby structure as in molds; it may be so dense as to be relatively hard and firm as in mushrooms; or there may be such a combination of density with firmness of cell walls as to produce a woody structure as in the bracket fungi (Fig. 714). Even in the woody forms, however, the fungi do not produce true tissues; in them the plant body is made up of interlacing hyphae, and the hyphae are single rows of cells.

Reproduction. The fungi may be reproduced vegetatively by the growth and division of the mycelium. The common or field mushroom, *Agaricus campestris*, is propagated for commercial purposes by cutting into blocks the substratum in which the mycelium is growing, and planting these blocks in new beds. In the fungi, as in the algae, the specialized reproductive bodies, other than the sexual cells themselves, are spores. In some of the simpler fungi the asexual spores are zoospores, but in the great majority they are non-motile spores enclosed in cell walls. The methods of sexual reproduction are very varied.

Distinguishing features. As the fungi are a very large and varied group, it is, as in the case of the green algae, very difficult to give a short description which will characterize all the members and exclude all other organisms. The presence of a mycelium is a very convenient distinguishing characteristic.

There are many other kinds of plants which do not have chlorophyll and are parasites or saprophytes. The mycelium of a fungus is readily distinguished from a bacterial filament by the larger size and more complex structure of the cells; like the algae and unlike the bacteria, they have definite and highly organized nuclei and cell walls which are easily seen. Many flowering plants lack chlorophyll and live as saprophytes or as parasites; these can be distinguished from the fungi not only by the absence of a mycelium but also because they, like other flowering plants, produce true tissues, have flowers, and reproduce by seeds.

Many algae resemble fungi in being composed of rows of single cells or coenocytic threads, but they are readily distinguished from the fungus mycelium by the occurrence of photosynthetic pigments.

Perhaps the plants which are most likely to be mistaken for fungi by one not familiar with botany are the *Myxomycetes*, which, as we have seen, form small fruiting bodies and resemble the fungi in lacking photosynthetic pigments and in reproducing by means of spores. They, however, can be readily distinguished from the fungi because they do not have a mycelium.

Distribution of fungi. Fungi occur throughout the world wherever conditions make life possible and there are materials on which they can grow. They are very abundant in soil, and occur on practically all kinds of decaying material. An enormous number are parasitic on plants, and they parasitize all types of plants from simple algae to the most advanced flowering plants. Many are parasitic or saprophytic on other fungi. There are also a considerable number which are parasitic on various types of animals, and quite a variety on man himself.

Importance of fungi. Many saprophytic fungi are harmful to man in that they cause spoilage of food and the destruction of other materials which are useful to him, as when they cause the decay of timber; however, like the saprophytic bacteria, they serve a most useful purpose in that they cause the breaking down of dead plant and animal matter and help return the component materials to the soil and air in forms which can be absorbed and utilized by green plants. The great majority of plant diseases are due to parasitic fungi, and these do tremendous damage; fortunately scientists have, in comparatively recent years, learned much about the control of these diseases, and the application of this knowledge has gone far toward minimizing the loss. A few human diseases are due to fungi; these are mostly of minor importance.

Classes of fungi. In the fungi there are three classes: the *Phycomycetes*, the *Ascomycetes*, and the *Basidiomycetes.*

CLASS *PHYCOMYCETES*

General characteristics. The *Phycomycetes*, as a class, bear considerable resemblance in general structure to the chlorococcine line of development in the green algae, and particularly to the *Siphonales.* While some of the simplest are unicellular, the great majority are coenocytic and have a much-branched mycelium in which there are many nuclei but no cross walls except in connection with the formation of reproductive structures. The nature of the mycelium is a very important diagnostic character in recognizing the *Phycomycetes*, as the *Ascomycetes* and the *Basidiomycetes* have a septate mycelium; that is, a mycelium which is divided up into separate cells by cross walls.

In the *Phycomycetes* there are three orders: the *Chytridiales*, the *Oomycetes*, and the *Zygomycetes.* The forms included in the *Chytridiales* are all small and the mycelium is never well developed. The *Oomycetes* and the *Zygomycetes* are characterized by a well-developed mycelium.

ORDER *OOMYCETES*

Saprolegnia

General characteristics. The *Oomycetes* are characterized by the fact that sexual reproduction is by the fertilization of eggs. In order to get an idea of this order we may consider a typical example, the genus *Saprolegnia.* This genus (Fig. 659) grows abundantly in water on decaying animal and vegetable matter, and sometimes on living animals. It is frequently very destructive to fish eggs and young fishes. The vegetative part of the plant consists of a branching system of filaments without cross walls. Some of these filaments enter the animal on which the plant is growing and absorb nutriment while others radiate out in the water and produce reproductive structures.

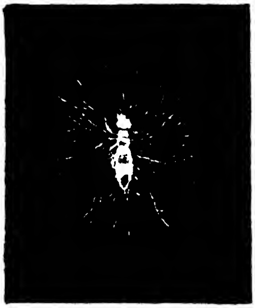


FIG. 659. Mycelium of *Saprolegnia* on an insect. (× 2½)

Reproduction. *Saprolegnia* reproduces asexually by the formation of zoospores with two flagella at the anterior end. These are produced in zoosporangia which are formed from the ends of club-shaped filaments (Fig. 660). The terminal portion of the filament is cut off by a cell wall, thus forming a zoosporangium, and the contents of this divide and round up to form zoospores. The zoospores escape through an opening at the tip of the sporangium.

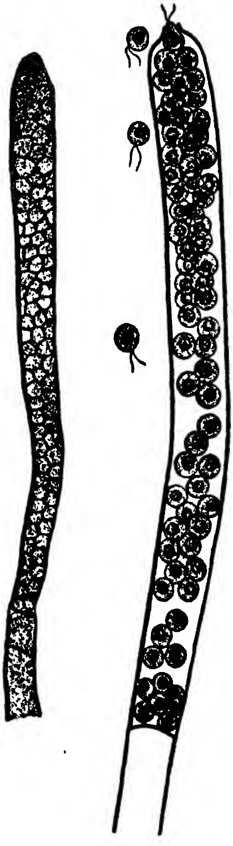


FIG. 660. Immature and mature zoosporangia of *Saprolegnia*. (× 230)

Following a period of motility, a zoospore comes to rest and surrounds itself with a new cell wall. After a time the protoplasm slips out of this wall and enters on a second period of motility. The zoospore is now kidney-shaped, with two flagella which are inserted on the side of the spore and not at the end as during the first period of motility. The significance of the two periods of motility with the different types of zoospores is not understood. At the end of the second period of motility the zoospore again surrounds itself with a cell wall, and germinates by sending out a tube which grows and becomes a mycelium.

Sexual reproduction is by means of oogonia and antheridia (Fig. 661). The oogonia are rounded structures which contain eggs and are cut off from the vegetative filaments by cross walls. The antheridium is a tubular branch which is cut off from the end of a hypha. It grows around an oogonium and produces branches (fertilizing tubes) which enter the oogonium and reach the eggs. In some cases a nucleus from an antheridium passes through the fertilizing tube, enters an egg, and fertilizes it (Fig. 662).

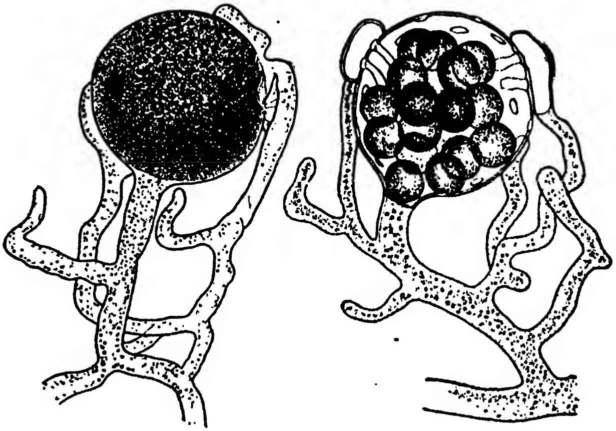


FIG. 661. *Saprolegnia monoica*

Left, young oogonium not yet cut off from vegetative filament, antheridia also not cut off from vegetative filament but in contact with oogonium; right, mature oogonium. Note numerous eggs and the fertilizing tubes growing from antheridia (× 250). After Pringsheim

Saprolegnia shows various degrees of loss of sexuality. In some cases, as just described, the eggs are fertilized by the antheridia. In other cases there are both eggs and antheridia, but the antheridia do not fertilize the eggs, the latter developing without fertilization. In still other cases no antheridia are formed.

Similarity of *Saprolegnia* and *Vaucheria*. The vegetative body of *Saprolegnia* is very similar to that of *Vaucheria* except that *Saprolegnia* lacks chlorophyll, whereas this is present in *Vaucheria*. In both cases the plant consists of branched, non-septate filaments. *Vaucheria* is attached to the substratum by means of a colorless branched filament known as a holdfast. *Saprolegnia* is attached in a similar way, except that the filaments enter the body of the animal on which the *Saprolegnia* is growing. The zoosporangium of *Saprolegnia* has a shape similar to that of *Vaucheria.* In *Saprolegnia* there is a zoospore for each nucleus, and each spore has two

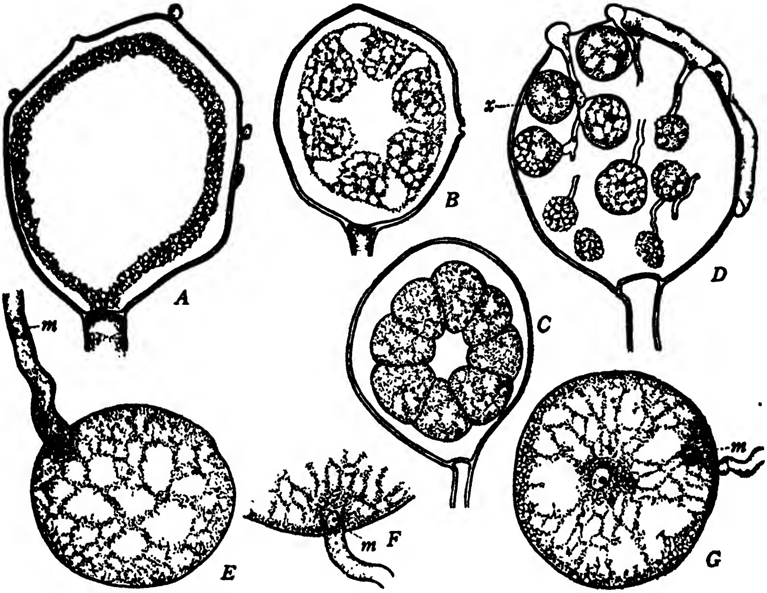


FIG. 662. *Achlya polyandra*, a relative of *Saprolegnia*

Development of eggs and discharge of male nuclei into egg as seen in sections. *A*, oogonium before the protoplasm has begun to divide up to form eggs. *B*, protoplasm dividing to form eggs. *C*, eggs already cut out from the protoplasm. *D*, eggs mature and fertilizing tubes (*x*) growing from antheridia to eggs. *E*, a fertilizing tube in contact with an egg; the male nucleus (*m*) is shown. *F*, male nucleus ready to be discharged into egg. *G*, an egg into which the male nucleus has been discharged; the egg nucleus is in the center of the egg. (*A–D*, × 400; *E–G*, × 1550). After Micke

flagella. The zoospore of *Vaucheria* has a different structure, but we have seen that there is reason to believe that it is a compound zoospore which can be regarded as formed by the fusion of a number of zoospores similar to those of *Saprolegnia.* The zoospore of *Vaucheria* has numerous pairs of flagella, each of which is opposite a nucleus, and the relatives of *Vaucheria* have biflagellate zoospores. The oogonia of the two forms are very similar except that

Saprolegnia usually has more than one egg, while *Vaucheria* usually has a single egg. The general form of the antheridia of *Saprolegnia* is likewise similar to that of the antheridia of *Vaucheria*; *Vaucheria*, however, produces sperms which swim through the water, while in *Saprolegnia* fertilization is by a tubular outgrowth from the antheridium. From the above comparison it will be seen that *Vaucheria* and *Saprolegnia* have a great many points in common.

Relationship. There has always been considerable difference of opinion among students of fungi as to various important aspects of the origin and evolution of the group to which *Saprolegnia* belongs. There are those who hold that the fungi represent a separate line of evolution which started with colorless flagellates and developed into the various classes of fungi which we know today. According to this point of view the similarities between *Saprolegnia* and *Vaucheria* would represent parallel development in different lines, just as there has been parallel development in various groups of algae. This point of view is supported by the fact that there are very simple fungi, apparently related to the *Myxomycetes*, which do not appear to be very far removed from flagellate ancestors. Also in the simplest order of *Phycomycetes*, the *Chytridiales*, there are various forms which have been interpreted as leading from the simplest fungi to the *Oomycetes*. It must be said, however, that the arrangement of the lower fungi in a series supposedly leading to such forms as *Saprolegnia* is nothing like so convincing as the series worked out in the green algae. In this connection it is well, however, to remember that many of our ideas as to evolutionary lines among the green algae are based on rather recent investigations.

There are two other general ideas as to the evolution of the fungi as a whole: first, that the fungi are a heterogeneous aggregation derived from various groups of algae; second, that the simplest fungi are related to the *Myxomycetes*, while all or most of the *Phycomycetes* and all of the *Ascomycetes* and *Basidiomycetes* represent one line of evolution derived from the green algae. Many botanists who hold one of these two views believe that *Saprolegnia* is descended from a siphonaceous green alga much like *Vaucheria*. This seems all the more possible because many different kinds of green plants have saprophytic or parasitic relatives. We find such plants scattered in a considerable number of families of flowering plants. If a holdfast of *Vaucheria*, instead of attaching itself to a rock, were to grow into the body of an animal and absorb nourishment, and if at the same time the plant were to lose its chlorophyll, we should certainly have a plant that would be very similar to some of the *Oomycetes*, such as *Saprolegnia*. We have already seen in the cases of certain flagellates that the same organism may, under different conditions, develop chlorophyll and manufacture its own food or lose its chlorophyll and live on organic matter. It is therefore not hard to believe that some plant similar to *Vaucheria* changed its mode of obtaining food and gave rise to the *Oomycetes*. The two types of zoospores in *Saprolegnia* are very puzzling from the evolutionary standpoint.

Albugo

General characteristics. Closely related to the family (*Saprolegniaceae*) to which *Saprolegnia* belongs is another family of the *Oomycetes* (*Peronosporaceae*) which contains a large number of species that are parasitic within the tissues of higher plants. These plants resemble the *Saprolegniaceae* in having much-branched coenocytic hyphae, and in having sexual reproduction by means of oogonia with eggs which are fertilized through fertilizing tubes that grow from the antheridia. Also, many of them produce zoo-

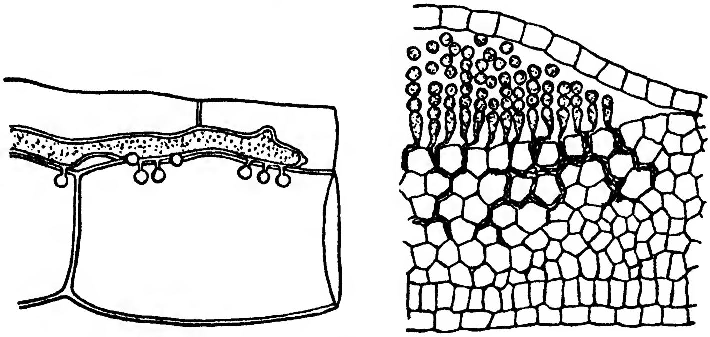


FIG. 663. *Albugo candida*

Left, a hypha with knoblike haustoria in cell of host (after De Bary). Right, section of a leaf showing development of conidiophores and conidia under the epidermis spores. This group of fungi causes many serious plant diseases. *Albugo* is parasitic on flowering plants. The hyphae are found in the intercellular spaces of the host. Knoblike haustoria grow from these hyphae into the cells of the host and absorb food material from them (Fig. 663).

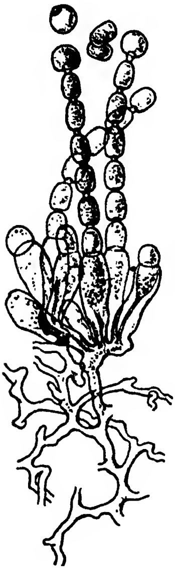


Fig. 664. Conidiophores bearing conidia, growing from mycelium of *Albugo*

Note the gelatinous disks separating the conidia. (×185). After Tulasne

Asexual reproduction. *Albugo* reproduces asexually by means of specialized sporangia which are shed as single cells and are usually called conidiospores or conidia. These are formed in chains on special branches known as conidiophores, so called because they bear conidia (Fig. 664). The conidiophores are formed in compact groups beneath the epidermis of the host (Fig. 663). They exert sufficient pressure to rupture the epidermis. The conidia of a chain are separated from each other by gelatinous disks which are formed by the gelatinization of the outer layer of the cell walls where the two cell walls come in contact. The conidia separate to form a dry product which may be scattered by the wind (Fig. 664). When the conidia germinate, they show that they are really modified zoosporangia. Under favorable conditions their contents divide up to form zoospores with two laterally inserted flagella (Fig. 665). Such a zoospore escapes from the conidium, swims about for a while, then comes to rest and sends out a hypha or germ tube which may infect a host and start a new *Albugo* plant.

Sexual reproduction. The sexual reproductive organs of *Albugo* bear considerable resemblance to those of *Saprolegnia,* except as to the number of oospores formed in an oogonium (Fig. 666).

The antheridium is much like that of *Saprolegnia.* A fertilizing tube grows from it into the egg. In some species there are numerous functional nuclei in the oogonium. In such cases numerous nuclei migrate through the fertilizing tube into the oogonium, where the male and female nuclei fuse in pairs. In other cases there is only a single functional female nucleus

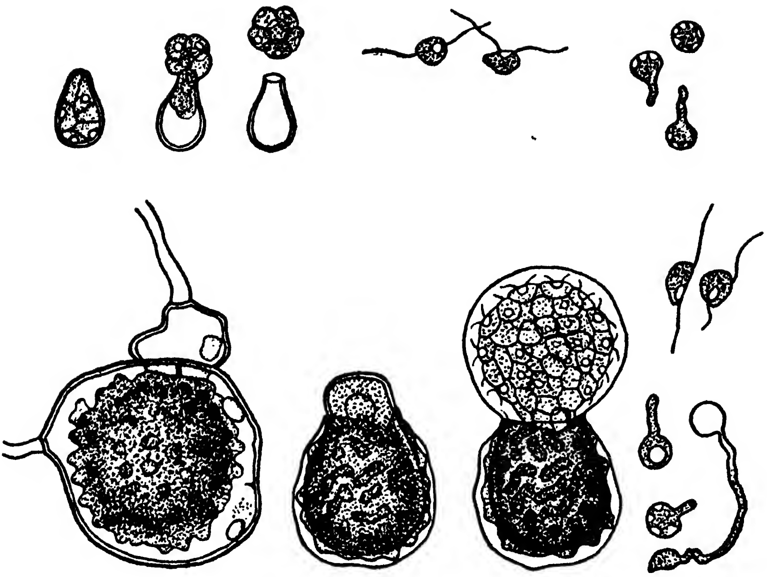


FIG. 665. *Albugo candida*

Formation, discharge, and liberation of zoospores. Above, from conidium; below, from an oospore. (× 400). After De Bary

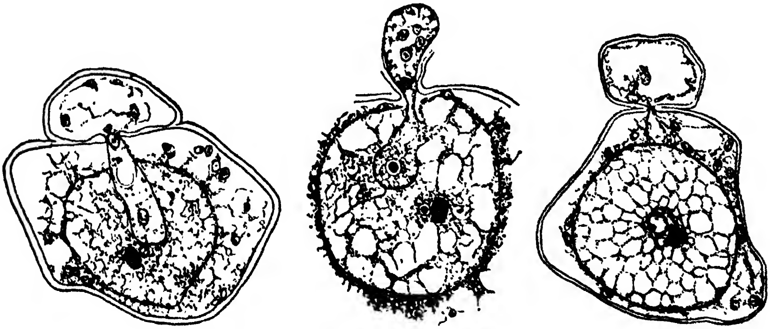


FIG. 666. Fertilization in *Albugo candida*

Left, fertilizing tube with male nucleus. The egg nucleus is just below the fertilizing tube, and to the left of the egg nucleus is the body known as the coenocentrum. This is formed by the condensation of protoplasm in the center of the oogonium. Its function is obscure, but it may serve to attract the nuclei. Center, fertilizing tube discharging its contents into the egg; right, egg and male nuclei fusing. (× 555). After Davis and only one male nucleus enters into the fertilizing tube and fuses with this (Fig. 666). The contents of the fertilized oogonium become transformed into an oospore. The wall of this consists of two layers, the outer of which is greatly thickened.

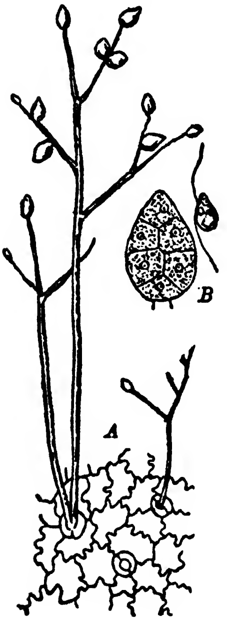


FIG. 667. Conidial fructification of the potato rot, or late blight (*Phytophthora infestons*)

A, conidiophores issuing from stomata and bearing conidia; *B*, at left, contents of a conidium divided to form zoospores; at right, a zoospore. (After Schenck)

The oospores are liberated by the disintegration of the tissues of the host. Under favorable conditions they germinate by producing biflagellate zoospores (Fig. 665).

Relatives of *Albugo*. *Albugo* is very distinctive in the manner in which its sporangiophores are arranged in groups beneath the epidermis and bear the sporangia in chains. In near relatives of *Albugo*, such as *Phytophthora*, the sporangia are borne on branched sporangiophores which project from the surface of the host (Fig. 667).

In some of the relatives of *Albugo* the transformation of sporangia into conidia has gone further than in *Albugo*. This is true in *Phytophthora infestans*, which causes a very serious disease of the potato, known as late blight. Here, depending on external conditions, the conidia may either produce zoospores or germinate directly by sending out a germ tube. In still other cases the conidia germinate only by sending out germ tubes.

ORDER *ZYGOMYCETES*

Rhizopus Nigricans

General characteristics. The members of the order *Zygomycetes* are distinguished from those of the order *Oomycetes* by their method of sexual reproduction. In the *Zygomycetes* there are no motile cells, and sexual reproduction is due to the conjugation of two hyphae.

Rhizopus is a typical example of the order *Zygomycetes*. This fungus is a conspicuous white mold which grows on bread and other substances. Its distribution is world-wide, and it is exceedingly common.

The vegetative body is a coenocytic mycelium composed of branching filaments (Fig. 668). The filaments are colorless, and, as is characteristic of coenocytic plants, they contain numerous nuclei and no cross walls. The main branches of the mycelium grow horizontally above the substratum, and are known as stolons. Where the tip of a stolon comes in contact with the substratum, it enlarges and the enlargement gives rise to branches. Slender much-branched filaments grow downward from the lower part of the enlargement and penetrate the substratum. They serve both as holdfasts to anchor the plant and for the absorption of nutriment material. From the upper portion several branches grow upward. These latter are unbranched, and each bears a sporangium at its tip. As they bear sporangia, they are called sporangiophores. Stolons also grow from the enlargements. Owing to this method of growth, the older plants have the appearance of sparingly branched stolons which, at intervals, produce enlargements bearing rhizoidal branches and sporangiophores. The general effect is something

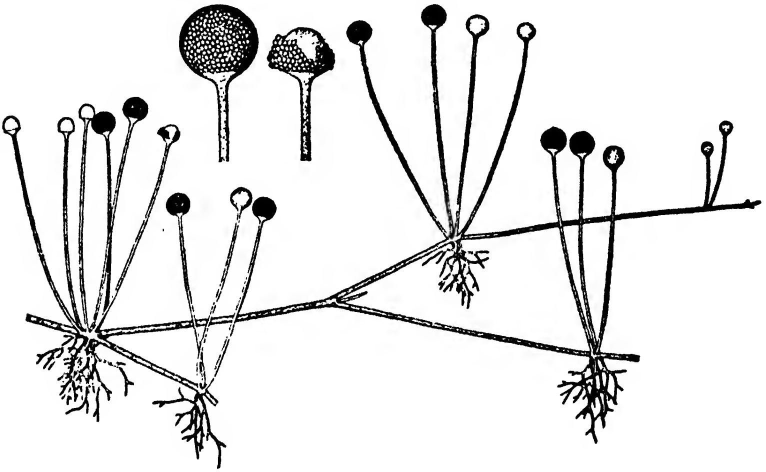


Fig. 668. *Rhizopus nigricans*

The main drawing shows the habit (× 25). Note the absorbing hyphae which enter the substratum, and the aerial ones which project upward and bear sporangia. Above are two sporangia, a ripe one containing spores and one from which many spores have been shed so that the columella is exposed (× 65) like that of a higher plant, such as a strawberry, which reproduces by means of runners or stolons.

Asexual reproduction. *Rhizopus* reproduces by means of spores, which are produced in very large numbers in the rounded sporangia. A sporangium is formed by the enlargement of the tip of a sporangiophore (Fig. 669). It is only the protoplasm in the outer part of the enlargement that divides up to produce spores. The spore-producing portion is therefore a cup-shaped sac, and surrounds a rounded sterile central portion known as the columella, which is continuous with the stalk of the sporangiophore. The spores germinate by sending out hyphae which produce mycelia.

As the tip of the sporangiophore enlarges to form a sporangium, the protoplasm in the peripheral portion of the enlargement comes to be fairly dense while that in the center is much less dense and is much vacuolated (Fig. 669). The spore-bearing portion is cut off from the columella in the following way: A series of small vacuoles appear just within the denser protoplasm, near where this joins the more vacuolated and central portion of the protoplasm. These vacuoles mark the region where the spore-bearing protoplasm will be separated from the columella. A cleavage furrow grows in from the periphery of the protoplasm near the base of the enlargement and joins with the above-mentioned vacuoles, which flatten and coalesce so that the protoplasm which will produce spores is separated from that of the columella. This is followed by the formation of a wall around the columella.

While the above-described process is going on, the protoplasm of the sporangium begins to divide up to form spores. This is brought about by cleavage furrows which start at the periphery of the protoplasm and grow inward. These divide the protoplasm into numerous small pieces, each of which contains several nuclei. Each piece surrounds itself with a cell wall and becomes a spore. The spores are scattered by the wind and are very plentiful in the atmosphere. They are so plentiful that it is easy to start a growth of *Rhizopus* by exposing a piece of moistened bread in an ordinary room. The bread should be covered, as by a glass vessel, so as to prevent the bread or the growth of *Rhizopus* from drying.

Sexual reproduction. The plants which produce sporangia and asexual spores may also reproduce by sexual fusion. Sexual reproduction is due to the conjugation of two similar filaments, which, however, always come from different plants. These conjugating filaments are short side branches, the tips of which grow together

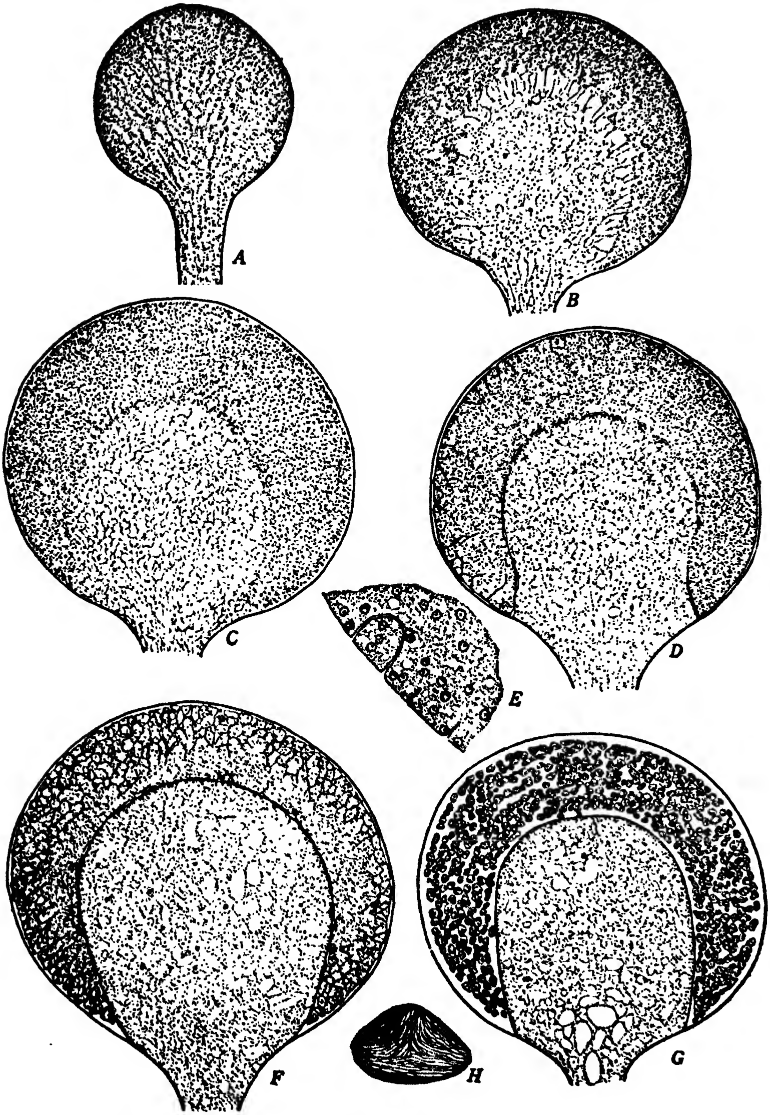


Fig. 669. Development of sporangium of *Rhizopus nigricans*

A, enlarged tip of hypha. *B*, outer and inner part differentiated. *C*, small vacuoles between outer and inner part. *D*, vacuoles elongating and coalescing; cleavage furrows starting from periphery. *E*, more enlarged view of nuclei and incipient cleavage furrows in protoplasm of sporangium. *F*, sporangium completely cut off from columella; more progress toward division into spores. *G*, mature sporangium. *H*, a spore greatly enlarged. (After Swingle)

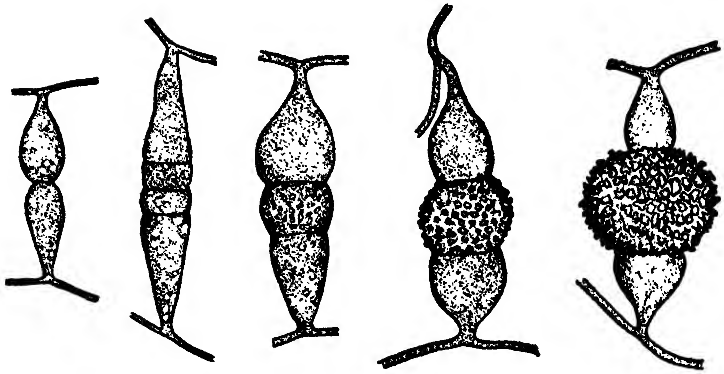


FIG. 670. Successive stages in conjugation and formation of a zygospore in *Rhizopus nigricans*. (× 80)

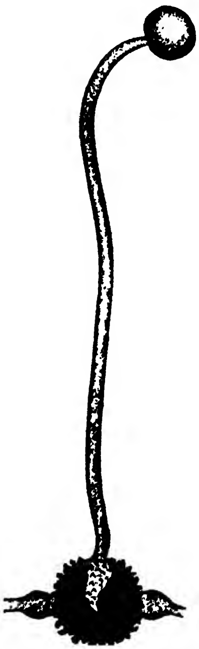


FIG. 671. Germination of zygospore of *Mucor mucedo*, a mold related to *Rhizopus*

Modified after Brefeld

(Fig. 670). The tips enlarge, and each is cut off by a cross wall. This is followed by the absorption of the walls separating the two terminal cells where these are in contact. These cells then fuse together to form a single cell. This enlarges, surrounds itself with a thick wall, and becomes a resting zygospore. The cells which fuse to form the zygospore may be regarded as gametangia which, instead of forming gametes, have taken over the function of gametes, and by their fusion form a large multinucleate zygote. When the zygospore germinates, the thick wall is burst and there grows out a hypha which becomes a sporangiophore with a single terminal sporangium containing asexual spores (Fig. 671).

While all the plants of *Rhizopus* look alike, there are in reality two kinds, as is shown by their action in sexual fusion. These two kinds are called + and —, and sexual fusion occurs only when a + and a — hypha come together. The existence of two kinds of plants which are alike in appearance but differ in sexuality is similar to the condition which occurs in some algae which we have considered previously. When ordinary vegetative plants reproduce asexually, the daughter plants are all the same kind as the parent plant. The occurrence of + and − strains is not confined to *Rhizopus* but is found in a considerable proportion of the molds. Species where there are + and − strains are said to be heterothallic. In some molds all plants appear to be alike, and there are no + and − strains; such species are homothallic. In heterothallic species the zygospore, as we have seen, is due to the fusion of a + and a − strain. Before the formation of spores in the sporangium which results from the germination of the zygospore, there is a segregation of the strains so that the spores formed in the sporangium have either a + or a − tendency.

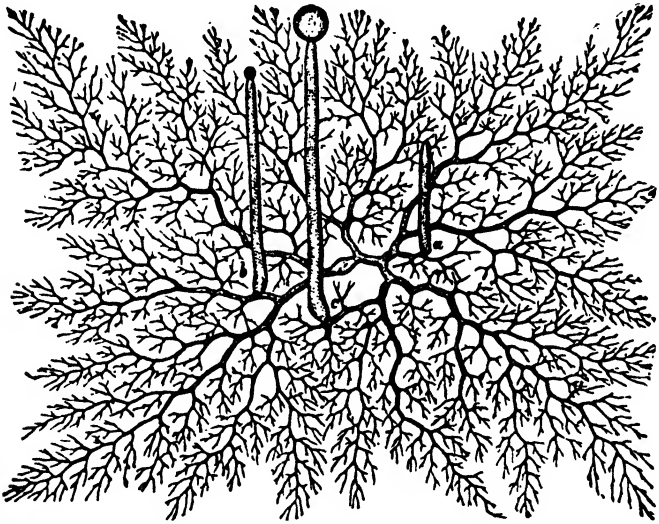


Fig. 672. The mycelium of a mold (*Mucor mucedo*) developed from a single spore

***a*, *b*, and *c*, erect branches which are to bear the sporangia, showing three stages of development. (After Brefeld)**

Relationship. The origin of the *Zygomycetes* is by no means clear. By those who regard the fungi as a very heterogeneous group derived from various kinds of algae it has been suggested that sexual reproduction by conjugation indicates that the *Zygomycetes* are related to the *Conjugales* among the green algae. However, the differences between the two groups are very great. The extensive development of coenocytic mycelia in both the *Oomycetes* and the *Zygomycetes* has suggested a relationship between these two groups. Perhaps the most generally accepted view is that the *Zygomycetes* are related to the simpler *Oomycetes* or the *Chytridiales*.

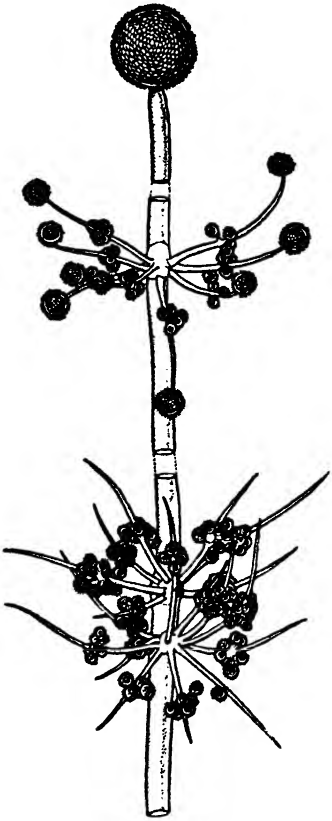


Fig. 673. *Thamnidium elegans*, one of the *Zygomycetes*

Note large terminal sporangium and sporangioles. (After Brefeld)

Relatives of *Rhizopus*. *Rhizopus* is one of a large number of molds which show considerable variation among them, particularly in the formation of the sporangia. In *Rhizopus* the sporangiophores are borne in clusters; in other cases they may be produced singly from the mycelium (Fig. 672). In some species the sporangiophores are unbranched, as in *Rhizopus*, while in others they may be much branched (Fig. 673). There are three general types of sporangia: large sporangia with many spores, as in *Rhizopus*, small sporangia (sporangioles) with few spores (Figs. 673, 674), and single-celled sporangia which act like spores and are known as conidia (Fig. 675). Some species have only one type, others two kinds, and still others all three. The sporangioles are modified sporangia, and the conidia represent a still further modification. Sporangioles are usually borne in larger numbers than sporangia, and conidia in still larger numbers.

Evolutionary trends in the *Zygomycetes*. In the development of the *Zygomycetes* from the more primitive to the more advanced forms there is a tendency for sporangia to be transformed into sporangioles and these into conidia. Forms like *Rhizopus* with comparatively few large many-spored sporangia, which are borne on unbranched sporangiophores, are regarded as the more primitive.

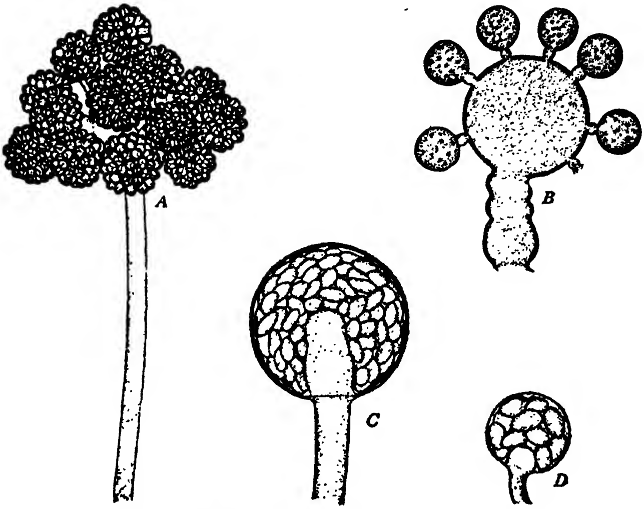


Fig. 674. *Blakeslea trispora*, one of the *Zygomycetes*

A, group of heads of sporangioles; *B*, section of a young head before development of spores; *C–D*, variations in size of sporangia. (After Thaxter)

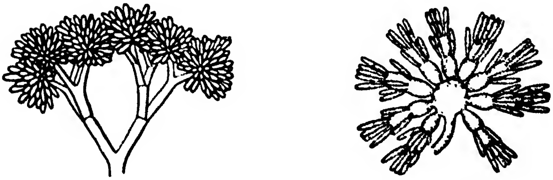


Fig. 675. Conidia of *Zygomycetes*

Left, *Piptocephalis freseniana* (× 250); right, *Dispua americana* (× 600). After Brefeld and Thaxter

These are followed by forms which have not only large many-spored sporangia, but also more numerous small sporangia. Finally there are forms with no sporangia and very numerous conidia. In the series there are monosporous sporangia that are really on the border line between sporangioles and conidia. The walls of the spore and the sporangium coalesce, but the sporangium wall is thrown off as an exospore on germination. In more advanced types of conidia the sporangium is entirely transformed into a conidium, there is no distinction between spore and sporangium wall, and the sporangium or conidium sends out germ tubes which produce a mycelium. Conidia may be formed singly on stalks or in chains. The true conidia, and also the conidiophores, are very similar to conidia and conidiophores found in the *Ascomycetes* and the *Basidiomycetes*.

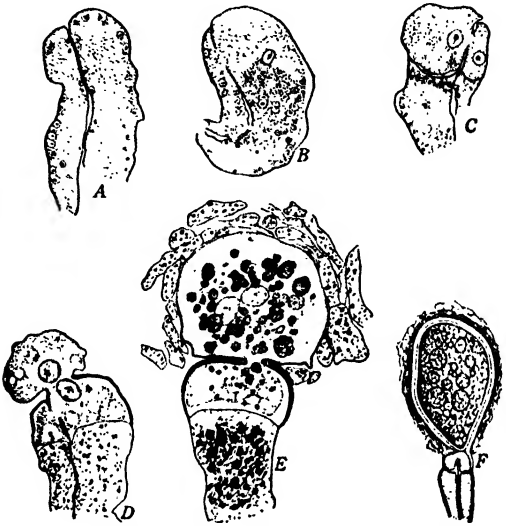


FIG. 676. ***Endogone lactiflua***, **a zygomycete with heterogamous conjugation**

A, large and small hyphae near each other; *B*, large and small hyphae are united through opening; *C*, uninucleate end cells have been formed from tips of hyphae; *D*, nucleus from smaller or male cell has migrated into larger or female cell, and both nuclei are migrating into an outgrowth of the larger or female cell; *E*, two nuclei in outgrowth from larger or female cell (this outgrowth will become the spore). (All × 400). *F*, spore of *Endogone tuberculosa*. (After Bucholtz and Thaxter)

Another trend in the *Zygomycetes* which has been interpreted as leading toward the *Ascomycetes* is a tendency toward increased septation in the more advanced *Zygomycetes*, particularly in older plants.

Still another development which has been interpreted as pointing toward the *Ascomycetes* is a tendency for an isogamous conjugation to become heterogamous (Fig. 676).

Empusa

General characteristics. The *Zygomycetes* contain a small family (*Entomophthoraceae*) of interesting fungi which are mostly parasitic on insects. They produce zygospores as the result of the conjugation of two filaments. To this group *Empusa* belongs (Fig. 677). One species of *Empusa* is very common on house flies, which are often fastened to window panes by hyphae. This species does not produce zygospores, but its conidia and other features are very characteristic of its group. A sporangium contains a single spore and is borne at the tip of an enlarged sporangiophore. The sporangiophores often project from the surface of a dead

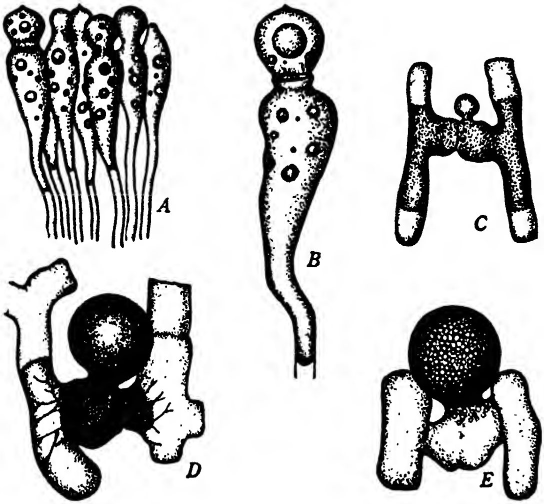


Fig. 677. *Empusa*

A, a group of conidiophores of *Empusa muscae* in various stages of development; *B*, mature conidiophore bearing a ripe conidium ready for discharge; *C–E*, *Empusa sepulchralis*, showing conjugation of two hyphae and outgrowth of zygospore. (*A*, *C–E*, × 170; *B*, × 335). After Thaxter

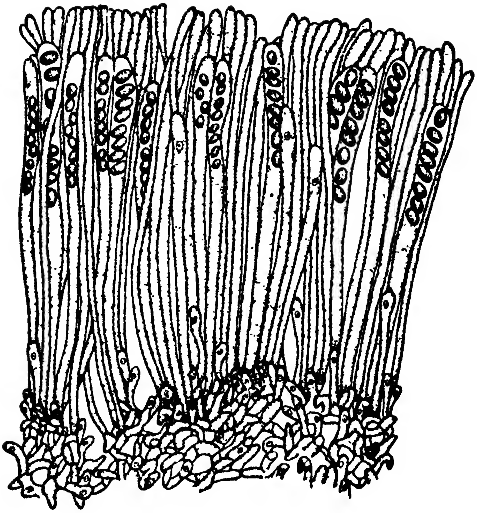


FIG. 678. Portion of hymenium of an ascomycete, *Lachnea* (see Fig. 680), showing asci in various stages of development and also paraphyses. (× 200)

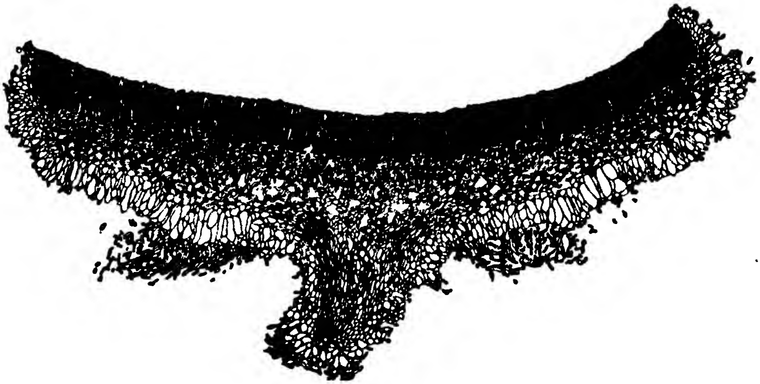


FIG. 679. Section of cuplike fruit body of *Lachnea*

Above is the hymenium composed of asci and paraphyses. (× 25) fly in sufficient numbers to form a sort of halo. A swelling of the sporangium and sporangiophore causes the bursting of the former and the forcible discharge of the spore. The spores germinate by sending out filaments.

CLASS *ASCOMYCETES*

General characteristics. The *Ascomycetes* are a very large and varied group of fungi which are characterized by having ascospores borne in asci. The ascus is a saclike, commonly cylindrical structure usually containing eight ascospores (Fig. 678), but the number of spores may vary from two to many. In a few cases the asci are

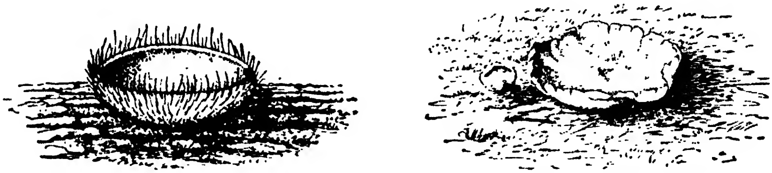


Fig. 680. Fruit bodies of *Lachnea* and *Peziza*

These are known as cup fungi on account of their shape. In both cases the hymenium covers the upper surface

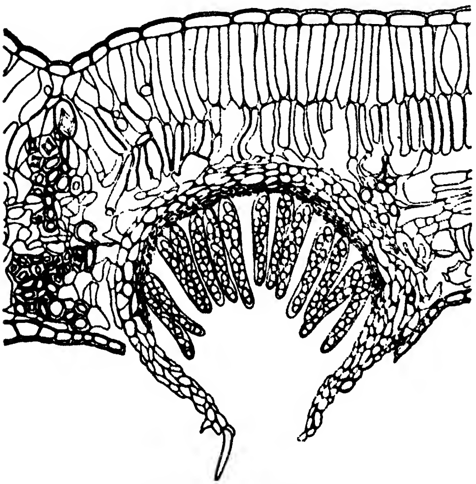


Fig. 681. ***Venturia inaequalis*** **(the causal organism of apple scab) on apple leaf**

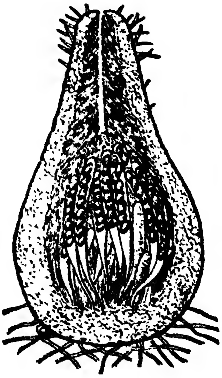


Fig. 682. Perithecium of *Podospora fimiseda*, a fruit body consisting of a single perithecium. (× 60)

After Tavel

borne singly, but in the vast majority of species they are produced in a layer, called the hymenium, which contains many asci, among which are the numerous sterile filaments, the paraphyses (Figs. 678, 679). In some cases the hymenium occurs as an outer covering of the fruit body (Fig. 680), while in others it lines flask-shaped cavities (Figs. 681, 682) called perithecia. Perithecia may occur singly (Fig. 682) or a considerable number may occur in one fruit body (Fig. 704). The fruit bodies of the *Ascomycetes* are known as ascocarps.

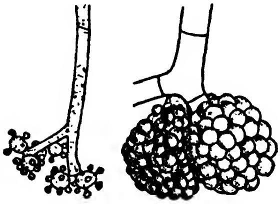


Fig. 683. Conidia of *Ascomycetes*

Left, *Lachnea abundans;* right, *Lachnea cretea.* (After Dodge and Gwynne-Vaughan and Williamson)

In addition to producing ascospores, many *Ascomycetes* also reproduce by conidia (Figs. 683, 700). Both the conidia and the conidiophores of the *Ascomycetes* bear considerable resemblance to those of the *Zygomycetes.* In many of the simpler *Ascomycetes* reproduction by conidia is much more prominent than reproduction by ascospores; in going from the simpler to the more highly developed forms this condition becomes reversed.

The *Ascomycetes* vary from small inconspicuous forms to others which are of considerable size and are fairly conspicuous. They never attain the large size of some of the *Basidiomycetes* such as the larger mushrooms and the huge bracket fungi.

Pyronema Confluens

General description. *Pyronema confluens* is one of the *Ascomycetes* which has been very thoroughly studied, and a consideration of its life history will serve as a very convenient introduction to the *Ascomycetes.* The ascocarp of *Pyronema confluens* is somewhat lens-shaped, pink or salmon-colored, and from one to three millimeters in diameter. The upper portion consists of a hymenium composed of asci and paraphyses. The ascocarps are found on material which has been burned or sterilized; and the fruit bodies are often confluent, from which characteristic it gets its specific name, *confluens.*

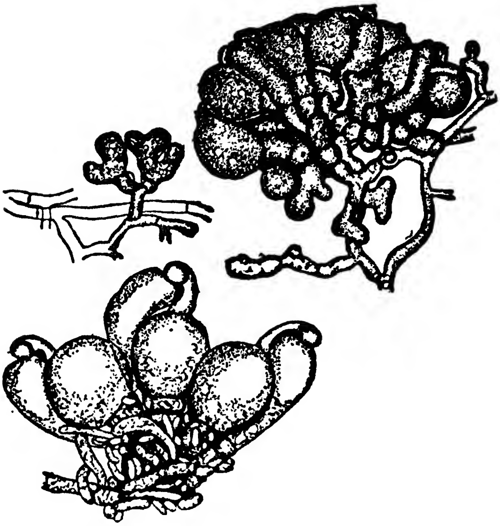


Fig. 684. Two stages in development of ascogonia and antheridia of *Pyronema confluens* (× 330) and a cluster of mature ascogonia and antheridia

After Claussen and Harper

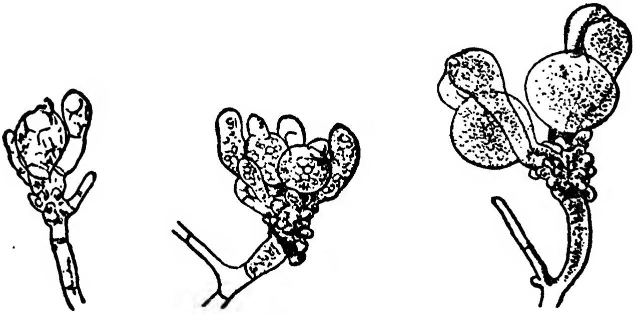


Fig. 685. Development of ascogonia and antheridia of *Pyronema confluens* and fusion of trichogyne with antheridium. (× 190)

After Thuret

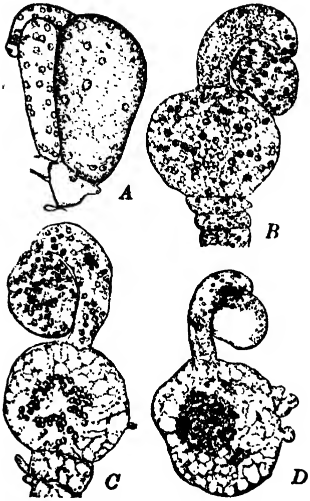


FIG. 686. Nuclear behavior in antheridia, trichogyne, and ascogonium of *Pyronema confluens*

A, the trichogyne growing from the archegonium on the right is in contact with the antheridium on the left. *B*, the trichogyne and antheridium have fused; the nuclei of the trichogyne have degenerated, while those of the antheridium are migrating into the trichogyne. *C*, late stage in migration of nuclei from antheridium into trichogyne. *D*, wall between trichogyne and ascogonium has disappeared so that there is open communication from the antheridium to the ascogonium. Note the beginning of the outgrowth of ascogenous hyphae on the right. (After Claussen and Harper)

Formation of sexual cells. The ascocarps of *Pyronema confluens* arise from multinucleate vegetative hyphae (Fig. 684). In the formation of an ascocarp usually a single hypha grows up and forks repeatedly. It is at first a unicellular coenocyte, but later becomes multicellular by the formation of cross partitions. The tips of some branches give rise to modified female oogonia known as ascogonia, and the tips of others to antheridia. Early in its development the ascogonium consists of a rounded terminal cell below which there are one to two stalk cells. The ascogonium sends out a papilla, or trichogyne, which develops to a considerable length and is cut off from the ascogonium by a cross wall. An antheridium grows up near an oogonium. The tip of the trichogyne comes in contact with the tip of an antheridium (Fig. 685).

Protoplasmic fusion in ascogonium. The ascogonium, trichogyne, and antheridium are all multinucleate. Where the tip of the trichogyne comes in contact with the antheridium, the walls of both are dissolved so that there is open communication between antheridium and trichogyne (Figs. 685, 686). The nuclei of the trichogyne, which have remained small, degenerate; and the nuclei from the antheridium migrate into the trichogyne. This is followed by the disappearance of the wall between the trichogyne and the ascogonium, after which the nuclei which came from the antheridium into the trichogyne continue their migration and enter the ascogonium. When this process is completed, a new wall is formed across the base of the trichogyne so that the ascogonium and trichogyne are again separated.

The nuclei which came from the antheridium through the trichogyne and those originally in the ascogonium become associated in pairs, each pair consisting of a male nucleus from the antheridium and a female nucleus produced in the ascogonium (Fig. 687).

Ascogenous hyphae. After the pairing of the nuclei in the ascogonium, large hyphae grow from the latter and into these the paired nuclei migrate (Fig. 687). These hyphae are called ascogenous hyphae, and it is they that give rise to the asci. During the growth and development of the ascogenous hyphae the nuclei remain in pairs. Two nuclei associated in this way form a dicaryon. When nuclear division occurs, the nuclei of a dicaryon divide simultaneously; thus one dicaryon gives rise to two dicaryons. When an ascus is finally formed it contains a dicaryon, the nuclei of which fuse to form the mother nucleus of the ascus (Fig. 688). The ascogenous hyphae are a very interesting phase in the life history of the *Ascomycetes*. They are somewhat similar to a diploid sporophyte. However, a diploid sporophyte results from the fusion

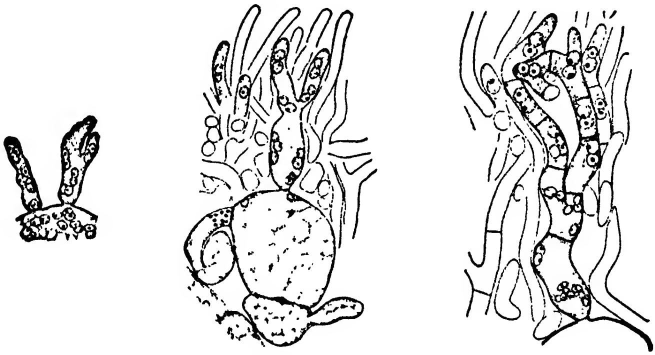


Fig. 687. Development of ascogenous hyphae of *Pyronema confluens*

Left, an early stage; note the nuclei in pairs. Center, a late stage. Right, a still later stage; note that the nuclei are still paired. (After Claussen) of two nuclei; in the case of the ascogenous hyphae there is, prior to their development, no actual fusion but only an association of nuclei. This association continues, and actual fusion is delayed,

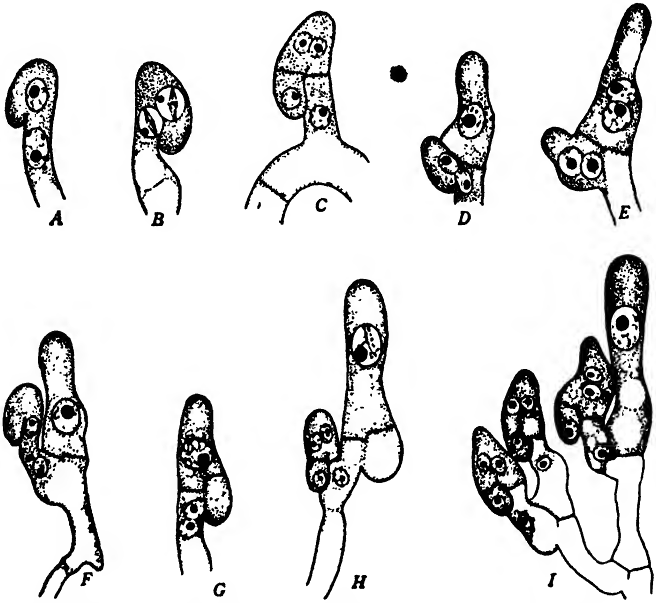


FIG. 688. Formation of ascus from tip of ascogenous hypha

A, the tip of the hypha is bent over; *B*, the two nuclei are dividing conjugately; *C*, three-cell stage of ascogenous hook (note uninucleate ultimate cell, binucleate penultimate cell, and uninucleate antepenultimate cell); *D*, the two nuclei in the antepenultimate cell have fused to form the primary nucleus of an ascus, the ultimate and antepenultimate cells have fused, and the nucleus from the antepenultimate is migrating into the ultimate; *E*, *F*, further stages in the development of the ultimate cell; *F*, a further stage in the development of the ascus; *G*, a stage similar to *D* except that the nucleus from the ultimate cell has migrated into the antepenultimate cell; *H*, further development of conditions seen in *G* (the ascus has developed further while the antepenultimate cell has produced a hook); *I*, three hooks and an ascus have developed from the binucleate tip of an ascogenous hypha. (After Claussen)

until just before the spores are formed. The number of chromosomes is reduced in the division of the ascus nucleus to form the nuclei of the ascospores.

Formation of asci. After the ascogenous hyphae are formed they continue to grow upward and branch, thus forming an extensive

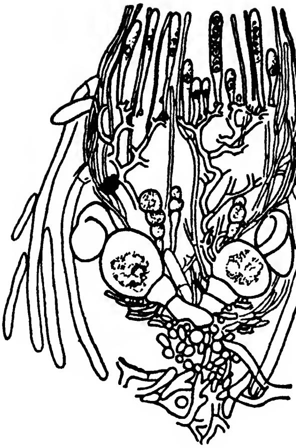


Fig. 689. Semidiagrammatic section of ascocarp of *Pyronema confluens*

In the drawing are shown two old ascogonia from which ascogenous hyphae have grown. Asci in various stages of development are shown at the ends of the ascogenous hyphae. Vegetative hyphae have grown up among the ascogenous hyphae and have given rise to paraphyses in between the asci. (After Harper)

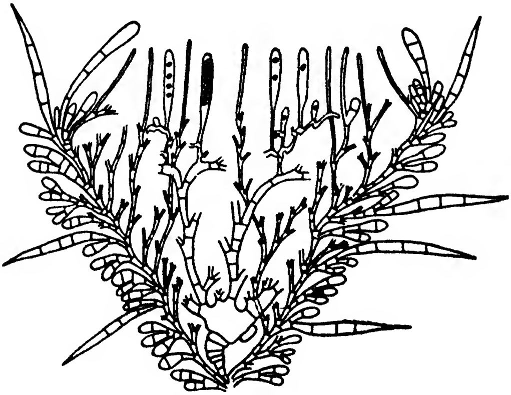


Fig. 690. Diagrammatic cross section of ascocarp of *Lachnea scutellata*

Ascogenous hyphae are shown growing from the ascogonium and bearing asci in various stages of development at their tips. Some of the branches of the sterile hyphae form an outer covering for the ascocarp, while others grow up among the ascogenous hyphae and form paraphyses branched system. At the tip of a hypha which is to form an ascus there is a dicaryon. The tip curls over to form a hook (Fig. 688). The two nuclei now divide simultaneously to form four nuclei. Walls come in between the sister nuclei so that there are formed a uninucleate antepenultimate cell, a binucleate penultimate cell, and a uninucleate ultimate cell. These compose the typical hook of the *Ascomycetes*. The two nuclei of the binucleate penultimate cell are not sisters, but the result of the continuation of the simultaneous or conjugate division of a dicaryon in the ascogenous hypha.

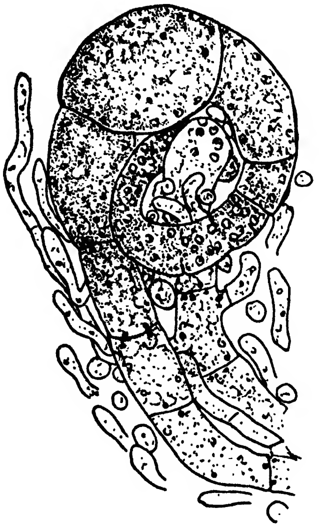


Fig. 691. Ascogonium and antheridium of *Ascobolus magnificus*

The antheridium, which is partially encircled by the trichogyne, is nearly empty. The trichogyne is multicellular, but the partial disappearance of cross walls between a number of the cells has opened a path for communication, through which the nuclei from the antheridium are migrating. (× 625). After Gwynne-Vaughan and Williamson

The two nuclei in the penultimate cell may now fuse and this cell be transformed into an ascus, or fusion may be still further delayed and the penultimate cell grow out to form another hook. In the meantime the ultimate and antepenultimate cells usually fuse and a nucleus of one migrates into the other. The binucleate cell may then send out a hypha which becomes a hook. In this way there may arise a considerably branched system of fused cells and hooks which will give rise to quite a number of asci.

Paraphyses. While the development described above has been going on, vegetative hyphae have grown up among the ascogenous hyphae and given rise to slender paraphyses among the asci (Fig. 689). Appearances indicate that the vegetative hyphae and paraphyses bring up food material which is absorbed from the paraphyses by the developing asci.

Sexuality in *Pyronema confluens*. In *Pyronema* and its relatives we see a tendency toward the degeneration of the sexual reproductive cells, a tendency which is manifest in various groups of the *Ascomycetes* and is continued in the *Basidiomycetes.* It is typical for *Pyronema confluens* to have a functional antheridium; but, depending upon the variety or conditions, an antheridium may be present and fail to function or it may be altogether absent. Under such conditions the ascogenous hyphae nevertheless develop from the ascogonium. The fusion of oogonia and antheridia is therefore not absolutely necessary for the formation of ascogenous hyphae. In some of the relatives of *Pyronema* an antheridium is never developed, but the ascogenous hyphae are formed from the ascogonium (Fig. 690). In still other forms there is an extreme condition in the degeneration of sexual cells where ascogenous hyphae arise directly from vegetative hyphae.

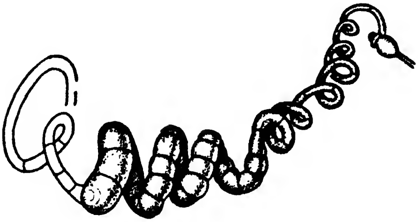


Fig. 692. Ascogonium of *Ascobolus carbonarius*

Note that the tip of the multicellular trichogyne is coiled around a conidium. (× 300). After Dodge

In some of the relatives of *Pyronema* the trichogyne is multicellular (Fig. 691), and in one (*Ascobolus carbonarius*) it appears to fuse with a conidium (Fig. 692).

The delay in nuclear fusion from the ascogonium to the asci, and the accompanying great development of ascogenous hyphae which produce many asci, have resulted in a very much larger number of nuclear fusions than there would have been had the sexual nuclei fused in the ascogonium. It has been suggested that the greatly increased number of nuclear fusions which has resulted from the extensive development of ascogenous hyphae compensates for the degenerations of the primary sexual cells themselves.

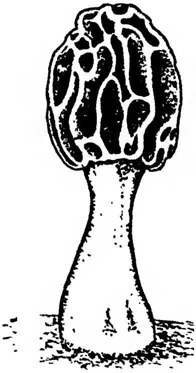


Fig. 693. Morel (*Morchella*)

The hymenium covers the upper portion of the ascocarp. (× ⅜)

Relatives of *Pyronema*. The ascocarp of *Pyronema* is known as an apothecium. At maturity the hymenium of an apothecium is exposed, and is a broad continuous layer, instead of being enclosed as in a perithecium. The order *Pezizales* includes a wide variety of fleshy forms in which the ascocarp is an apothecium. These fungi are frequently called cup fungi, because the ascocarp is often cup-shaped (Fig. 680) or disk-shaped as in *Pyronema*. The ascocarp may be with or without a stalk. In some forms the fertile portion, instead of being cup-shaped or disk-shaped, may be knob-shaped or club-shaped; and in the edible morels the ascocarp is club-shaped with the fertile portion much folded or indented (Fig. 693).

Origin of *Ascomycetes*. In the case of the *Ascomycetes*, just as in cases of other groups of fungi which we have considered, there is divergence of opinion as to their evolutionary history. Those who believe that the fungi are a heterogeneous group derived from various classes of algae are inclined to the belief that the *Ascomycetes* are descended from the red algae. Other authorities believe that they have been derived from the *Zygomycetes*. These views we will discuss later.

Hemiascomycetes

General characteristics. The *Hemiascomycetes* are characterized by a very simple structure and the lack of ascogenous hyphae. Sexual reproduction is due to the conjugation or fusion of two cells. In some cases the fusing cells are alike; in others they are unlike, and may be regarded as male and female, as the nucleus from the smaller cell migrates into the larger (Fig. 694). The cell formed by the fusion may become an ascus (Fig. 694) or grow out to produce an ascus (Fig. 695).

***Dipodascus*.** Perhaps the most primitive of all known *Ascomycetes* is *Dipodascus*. The hyphae of *Dipodascus* are branched and composed of multinuclear cells. The sexual reproductive cells are formed by the putting forth of tubes by two neighboring cells (Fig. 695). In the course of their development one becomes larger than the other. This acts as a female cell. In both the male and the female cell there are fairly numerous nuclei, but only a single nucleus of the male cell becomes differentiated as the male nucleus. This migrates into the female cell, where also there is only a single nucleus differentiated as a sexual nucleus. The two sexual nuclei fuse, and the cell grows out to form an elongated ascus. The fusion nucleus divides to form numerous nuclei, each of which becomes the nucleus of an ascospore.

Similarities between *Ascomycetes* and *Zygomycetes*. There are numerous striking points of similarity between the higher *Zygomy-*

cetes and the simpler *Ascomycetes*. Many of the simpler *Ascomycetes* are characterized by an abundant production of conidia, and both the conidia and conidiophores are very similar to those of the higher *Zygomycetes*.

Sexual reproduction in the higher *Zygomycetes* is also very similar to that of some of the *Hemiascomycetes*. In both cases we note the fusion of unequal cells in each of which there is a single functional sexual nucleus (compare Fig. 676 and Fig. 694). In *Dipodascus* the female cell grows out to form an ascus (Fig. 695); in some of the higher *Zygomycetes* it may grow out to form a thick-walled spore (Fig. 676). Such facts as the above have been interpreted as showing that the *Ascomycetes* represent a further development of evolutionary tendencies found in the *Zygomycetes*.

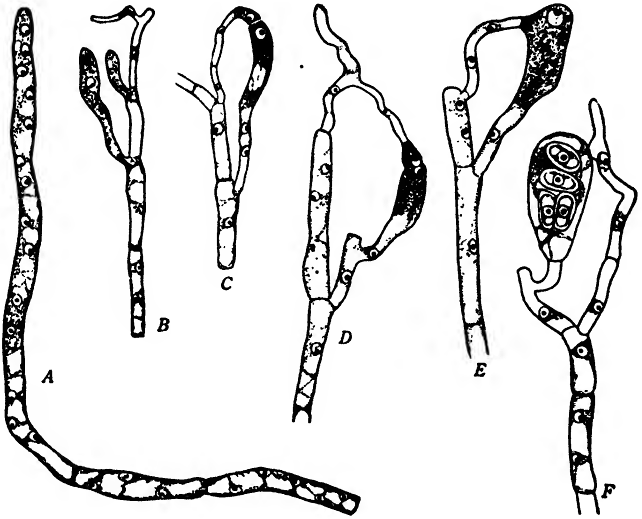


FIG. 694. *Endomyces magnusii*, one of the *Hemiascomycetes*

A, a hypha; *B*, early stage in development of sexual cells; *C*, male and female cells ready for fusion; *D*, cells have fused; *E*, male and female nuclei have fused; *F*, ascus with four spores formed from fertilized female cell. (After Guilliermond)

There is a good deal of similarity in the general character of the mycelia of the two groups. In the more primitive *Zygomycetes* a plant is a large single-celled coenocyte, but in some of the more advanced forms there is a tendency towards the development of septation. In the *Ascomycetes* the hyphae are septate, but multinucleate cells are very characteristic of the group. The development of septation in the hyphae of the *Ascomycetes* may be similar to the derivation of the *Siphonocladiales* from the *Siphonales* by increased septation.

In the *Zygomycetes* we noted a change from many-spored sporangia to sporangioles, and then to conidia.

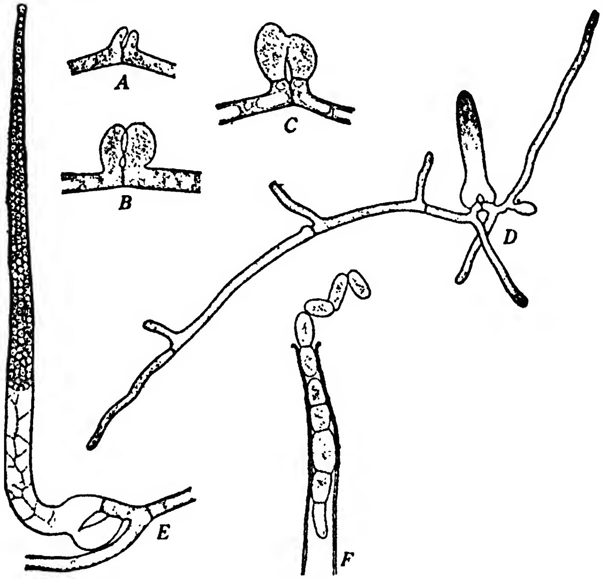


FIG. 695. *Dipodascus albidus*

A–C, fusion of large and small cells; *D*, habit of plant and formation of ascus; *E*, ascus with spores; *F*, escape of spores. (After Lagerheim)

The fusion of male and female gametangia in the *Ascomycetes* has been interpreted as a continuation of a development of heterogamy initiated in the *Zygomycetes* (Fig. 676).

In some of the higher *Zygomycetes* nuclear fusion does not follow immediately after the fusion of the larger and smaller cells, but takes place in an outgrowth from the larger cell (Fig. 676). This has been interpreted as a tendency toward a delay in nuclear fusion, a continuation of which has resulted in the development of ascogenous hyphae, conjugate division, and a delay of nuclear fusion until the ascus.

Yeasts

Yeasts are microscopic plants belonging to the genus *Saccharomyces* and related genera, and are included in the *Hemiascomycetes*. They are essentially unicellular and uninucleate plants, but may form chains or irregular groups of cells (Fig. 696). They are particularly interesting on account of their method of obtaining energy and also because of their great economic importance. Yeast plants obtain energy by converting sugar into alcohol and carbon dioxide, a process which is known as alcoholic fermentation. This process is the basis of the commercial manufacture of ethyl or grain alcohol and of alcoholic drinks. Yeast is also used in raising bread, and for this purpose is sold in the form of yeast cakes. The fungus causes the sugar in the bread to be converted into alcohol and carbon dioxide, and it is the production of the carbon dioxide that is responsible for the formation of holes in the bread.

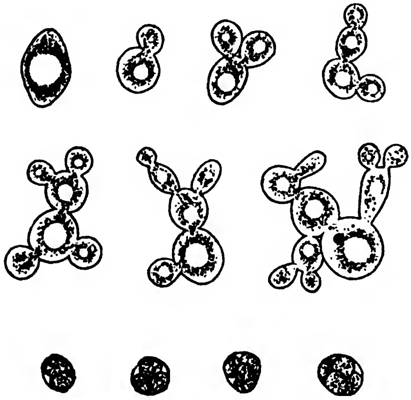


Fig. 696. Yeast (*Saccharomyces*), showing single cell, budding cells, and the formation of ascospores in cells. (× 960)

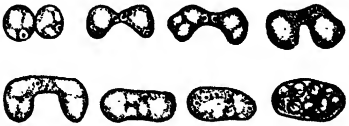


Fig. 697. *Schizosaccharomyces octosporus*

Upper line shows fusion of two cells; in the last figure the two nuclei are fusing. Lower line shows the development of ascus: the single fusion nucleus first divides to eight, and the eight ascospores are cut out. (After Guilliermond)

Reproduction. A very common and easily obtained yeast is the beer yeast, *Saccharomyces cerevisiae*. When the plant is not in active growth it consists of single cells. Asexual reproduction is by budding. In this process a protuberance grows from the parent cells and is constricted off, thus forming a new individual. A daughter cell may begin to bud before it has been constricted from the parent cell, and in this way chains or irregular masses of cells may be formed (Fig. 696).

Under certain conditions the contents of the cell may divide to form four spores. The whole cell is then interpreted as an ascus and the spores as ascospores (Fig. 696). Connecting links between this type of ascus-formation and that found in the previously discussed forms of *Hemiascomycetes* are afforded by species of yeast in which there is sexuality. In these, two cells fuse and the fusion product becomes an ascus with ascospores (Fig. 697). We thus find in yeast a tendency toward the degeneration of the sexual process, analogous to a similar tendency noted in *Pyronema* and its relatives.

Aspergillus and *Penicillium*

General characteristics. The genera *Aspergillus* and *Penicillium* are among the simplest of the true *Ascomycetes*. In them reproduction by conidia borne on conidiophores is much more abundant than reproduction by ascospores. In *Aspergillus* the conidiophore has a rounded tip from which radiate filaments that produce rows of spores. There are very common species which have green,

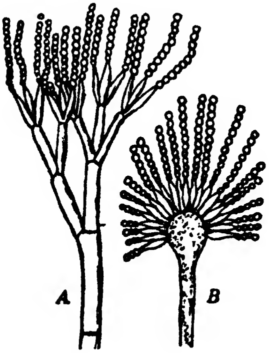


FIG. 698. Green and yellow molds

A, the green mold (*Penicillium*); *B*, the yellow mold (*Aspergillus*)

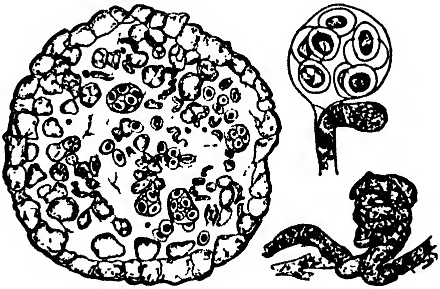


FIG. 699. *Aspergillus herbariorum*

Left, section of perithecium. In the perithecium are seen sections of the asci irregularly arranged. Upper right, a single ascus. By comparing this with the left figure, the asci can be located. Lower right, sexual filaments. (After Fraser and Chambers) black, or yellow conidia and are known as green, black, or yellow molds. The growth of these molds is very much shorter and more compact than that of *Rhizopus nigricans.* The conidia of *Penicillium* are borne in chains at the end of branched conidiophores. *Penicillium* is usually some shade of green, and, like *Aspergillus,* is very common. One or the other of these genera is very frequently found as a coating on a great variety of organic substances, including bread, cheese, rotting fruits, jams, preserves, and leather.

The particular characteristics which appear in Roquefort and Camembert cheeses are due to the growth of *Penicillium roqueforti* and *Penicillium camemberti* respectively. *Penicillium roqueforti* can be readily distinguished in Roquefort cheese by its green color, while *Penicillium camemberti* is seen as a whitish covering around a Camembert cheese. The soft consistency of Camembert cheese is due to enzymes secreted by the mold.

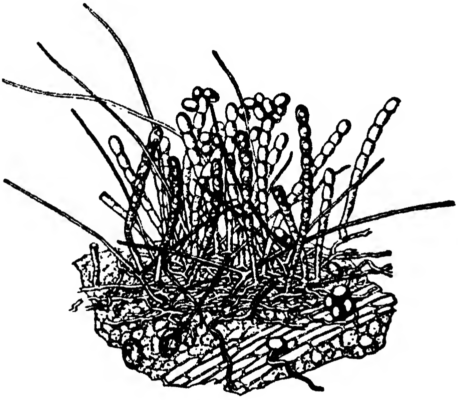


Fig. 700. ***Erysiphe pannosa***
Conidiophores producing conidia on the surface of the leaf. (After Tulasne)

The ascocarp of *Aspergillus* and *Penicillium* consists of a small and simple perithecium which is without an opening and in which the asci are irregularly distributed (Fig. 699). The formation of the ascocarp is initiated by two simple similar filaments which coil around each other and appear to fuse (Fig. 699).

Powdery Mildews

The powdery mildews are parasites on the leaves of higher plants. The mycelium grows on the surface of the leaf and sends out haustorial branches which penetrate the cells of the leaf and absorb nutrition material. Early in the season they produce conidia borne on conidiophores (Fig. 700). These are often so

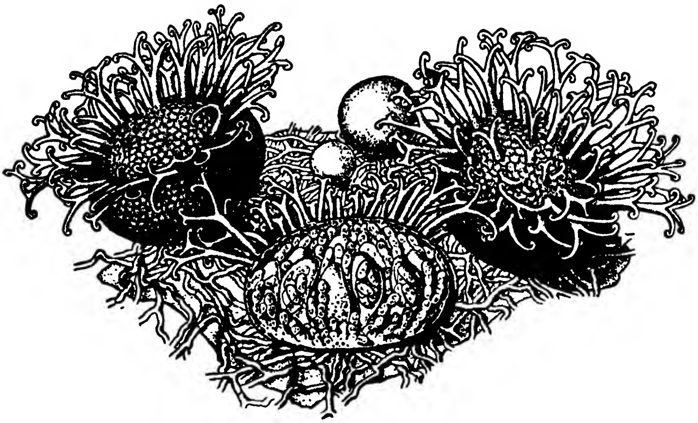


Fig. 701. Perithecia of *Erysiphe*, one of which is shown in section

After Tulasne

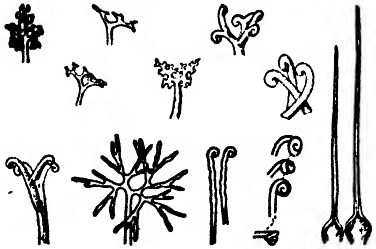


Fig. 702. Appendages from the perithecia of various species of powdery mildews

After Salmon and Tulasne

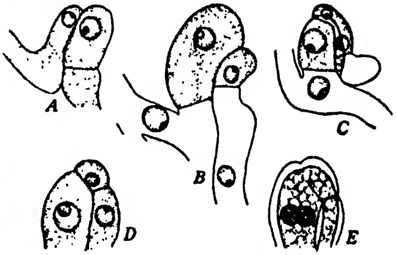


Fig. 703. Ascogonium and antheridium of *Sphaerotheca castagnei*, one of the powdery mildews

A, the ascogonium is to the right; *B*, the ascogonium is to the left; *C*, the antheridium mother cell is binucleate; *D*, the antheridium is cut off; *E*, the antheridium nucleus has migrated into the ascogonium. (After Harper)

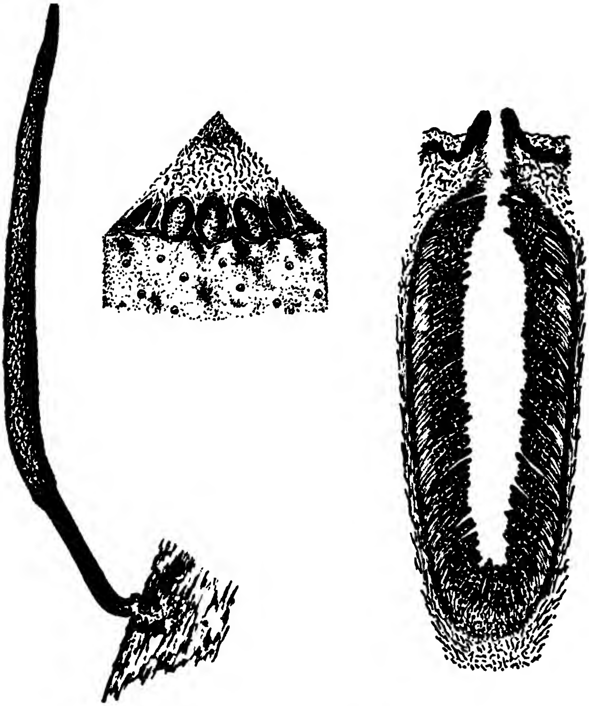


Fig. 704. ***Xylaria*, an ascomycete**

Left, a whole fruit body (× 1). Center, combined cross section and surface views of a portion of a fruit body, showing perithecia (× 12). Right, section of a perithecium showing hymenium; note asci in hymenium (× 65)

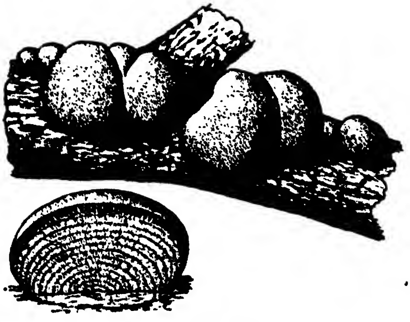


Fig. 705. ***Daldinia***

Ascocarps growing on a dead branch (× ½); below, section through an ascocarp showing numerous perithecia in the outer layer (× 1)

abundant as to give the leaf the appearance of being dusted with powder. This leads to the name "powdery mildews."

Ascocarps are usually formed later in the season than the conidia. The ascocarp is a single perithecium without an opening (Fig. 701). Within the perithecium there is a single ascus, or a few asci arranged in a compact group and not scattered irregularly as in *Penicillium* and *Aspergillus*. Some of the cells of the covering of the ascocarp grow out and form long characteristic appendages (Figs. 701, 702). These appendages are one of the most convenient features for distinguishing different species.

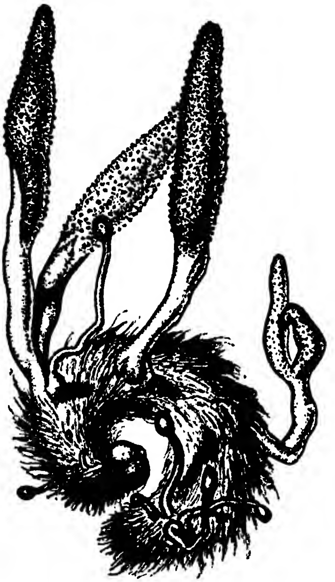


Fig. 706. *Cordyceps militaris* on a dead caterpillar

After Tulasne

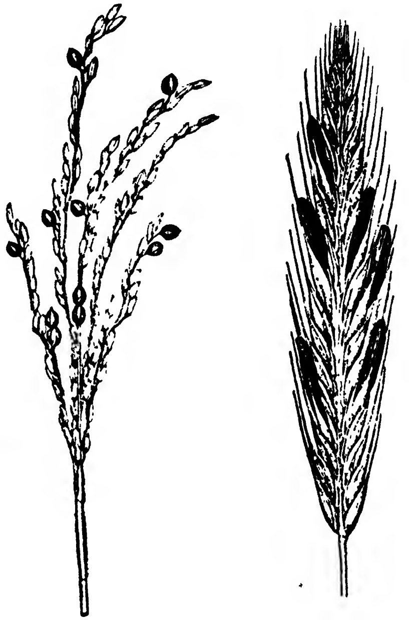


Fig. 707. Parasitic ascomycetes

Left, *Ustilaginoidea virens*, an ascomycete parasitic on rice (*Oryza sativa*) (× ⅓); right, ergot (*Claviceps purpurea*), an ascomycete parasitic on rye (× ⅔). In both cases the black bodies are produced by the fungus

The vegetative cells are uninucleate, as are also the ascogonia and antheridia. The ascogonium is a somewhat oval cell, while the antheridium is a small cell cut off from the end of a branch (Fig. 703). Where the antheridia and ascogonia come in contact, an opening is formed between the two by the dissolving of the cell walls and the nucleus from the antheridium migrates into the ascogonium. An ascogenous hypha is produced by the ascogonium, and this gives rise to the asci. While in some of the powdery mildews there is a functional antheridium, in others the antheridium appears not to function, and so there would seem to be an indication of the degeneration of the sexual cells such as was noted in other groups of *Ascomycetes*.

ASCOMYCETES WITH OPEN PERITHECIA (BLACK FUNGI)

Among the *Ascomycetes* there are a tremendous number which have perithecia with a definite opening through which ascospores are discharged. All these are sometimes placed in a single group, the *Pyrenomycetes*, sometimes called "black fungi" because several species of them produce black or blackish masses. In some cases the ascocarp consists of a single perithecium, while in others

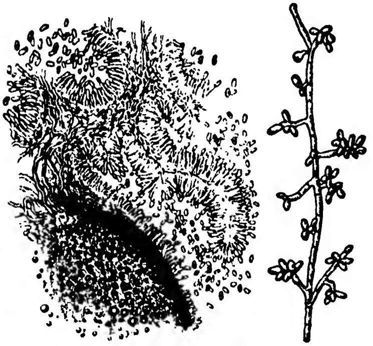


FIG. 708. *Claviceps purpurea*

Left, section of conidial stage before the formation of the horny sclerotium. (After Tulasne.) Right, formation of conidia in a culture. (After Brefeld from Tavel)

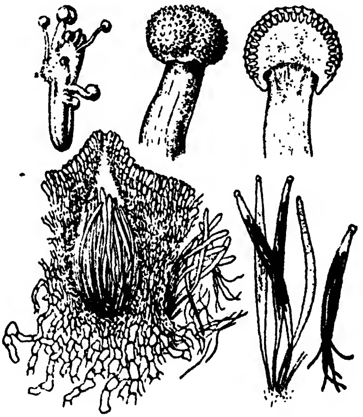


FIG. 709. *Claviceps purpurea*

Upper left, perithecial heads growing from sclerotium; center, perithecial head; right, section of perithecial head showing numerous perithecia; lower left, section of a perithecium showing asci; lower right, asci and ascospores. (After Tulasne) it may contain very numerous perithecia. One of the most conspicuous of this group is *Xylaria*, which is very common on rotten wood (Fig. 704). It forms long club-shaped or branched ascocarps, in the surface of which are embedded very numerous perithecia.

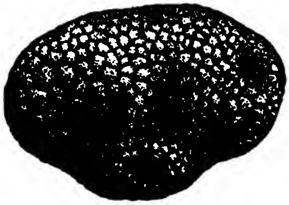


Fig. 710. Truffle (*Tuber brumale*), an edible fungus in which the ascospores are enclosed in a sterile covering. (× $\frac{2}{3}$)

Claviceps purpurea. *Claviceps purpurea* is known as ergot. It is very interesting not only because it is parasitic on various grasses, particularly on rye, but also because it furnishes an important medicine (Fig. 707). The ascospores infect the ovaries of the host plant and form a mass of hyphae which produce conidia (Fig. 708). Later the production of conidia ceases, and the hyphae produce an elongated hard structure known as a sclerotium (Figs. 707, 709). It is this sclerotium that is used in medicine. The sclerotium persists throughout the winter. In spring, when sufficient moisture is present, it begins to grow by sending out columns of hyphae at the ends of which perithecial heads are formed. Many perithecia are developed in the periphery of the head, and each contains numerous ascospores (Fig. 709).

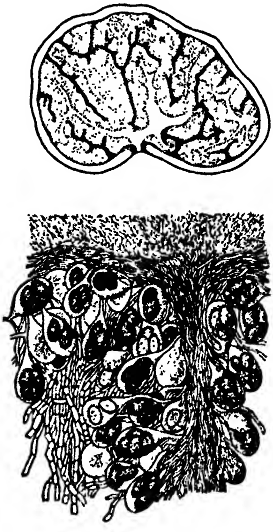


Fig. 711. Truffle (*Tuber rufum*)

Above, section of the truffle (× 3); below, section of small portion showing asci (× 250). After Tulasne from Tavel

Truffles

The truffles are a genus of tuberous *Ascomycetes* which are developed underground, and in which the asci are developed within the ascocarp (Figs. 710, 711). Several of the species are highly valued as articles of food. In France the gathering of truffles is an important industry, and large areas have been reforested with trees around the roots of which truffles grow. The export of truffles from France before the World War amounted to as much as fifteen million dollars a year.

• *Laboulbeniales*

This is a small group of minute *Ascomycetes* none of which are more than a millimeter in length. They grow attached to living insects. A few of them send haustoria into the insect, but most of them do not. Fig. 712 shows a typical plant with a female branch to the left and a male branch to the right. On the male branch are seen a number of antheridia, from three of which naked non-motile male cells are escaping. In the center of the female branch is seen an ascogonial cell, above which is another large cell, and above this a trichogyne which projects as a long slender protuberance at the tip of the branch. Male cells from the antheridium come in contact with the trichogyne and cling to it. It has been presumed that a nucleus from a male cell migrates down through the trichogyne and intermediate cell into the ascogonium cell, although such a migration has not been demonstrated. In some species no male cells are produced. The ascogonial cell sends out branches which produce asci.

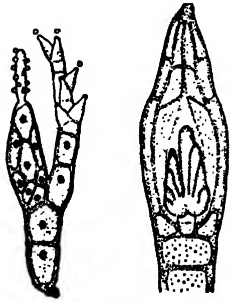


FIG. 712. *Stigmatomyces baerii*, one of the *Laboulbeniales*

Left, a plant with female branch to the left and male branch to the right; right, a perithecium in which asci are developing. (After Thaxter)

Relationship of *Ascomycetes*

The chief interest in the *Laboulbeniales* lies in the likeness which many have seen in them to the red algae. The perithecium of the *Laboulbeniales* has been considered as similar to the cystocarp of the red algae. Other points of similarity are seen in the trichogynes and in the non-motile male cells which are formed in antheridia and are caught on the trichogynes. If, as has been presumed, there is a migration of a nucleus from the male cell through the trichogyne to the carpogonial cell, this is still another point of similarity. The method by which the branches which give rise to the asci are formed from the ascogonium also shows certain points of resemblance to the formation of branches which produce carpospores in the red algae. Owing to all the above similarities, it has been believed by many botanists that the *Ascomycetes* are descended from the red algae through forms having many points in common with the *Laboulbeniales*.

The above view is diametrically opposed to that which holds that the *Ascomycetes* are descended from the *Zygomycetes*. Adherents of the latter view claim that while superficially there is considerable resemblance between the reproduction of the red algae and that of the *Laboulbeniales*, the details are very different, and that the *Laboulbeniales* are much closer to the *Ascomycetes* than to red algae. It is pointed out that the method of ascospore formation is entirely different from anything known in the red

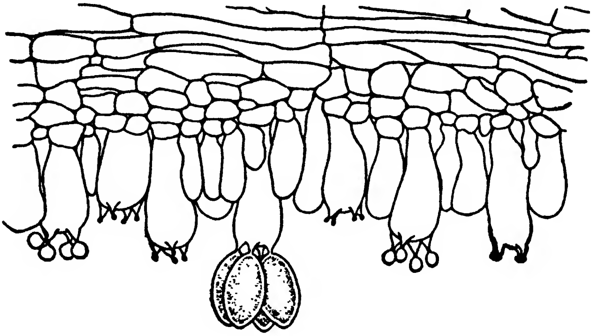


Fig. 713. Portion of hymenium of a mushroom, showing basidia of different ages. (× 860)

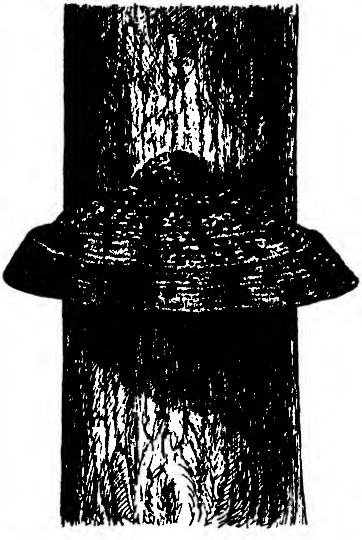


Fig. 714. A pore fungus (*Fomes pachyphloeus*) on a tree trunk. (× $\frac{2}{15}$)

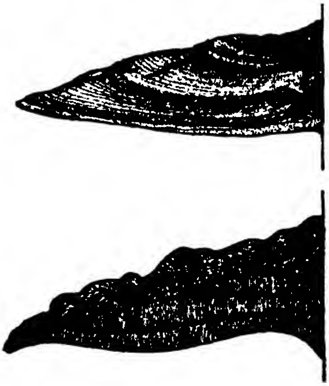


Fig. 715. Side view and section of a pore fungus (*Fomes pachyphloeus*) The layers in the lower drawing show pores formed during successive seasons. (× $\frac{1}{8}$)

algae. The male cells are regarded as modified conidia; and the fertilization by means of conidia is explained as being connected with the degeneration of sexual cells, conidia having taken the place of the antheridia.

In one of the *Ascomycetes* related to *Pyronema* (*Ascobolus carbonarius*) there is evidence for the fertilization of ascogonia by conidia, and in the lichens by conidiumlike spermatia (Fig. 777). In these, as in the *Laboulbeniales*, nuclear migration into the ascogonium has not been demonstrated.

In building up the theories of evolution within the *Ascomycetes* there is a great similarity in the forms and structures used, and much the same series results, except that the series is read in opposite directions.

The theory that the *Ascomycetes* are descended from the *Zygomycetes* has been discussed previously. According to this theory the sexual fusion in the *Hemiascomycetes* is derived from that in the higher *Zygomycetes*, while the typical ascogonia and antheridia of the *Ascomycetes* are the development of the sexual cells of the *Hemiascomycetes*. The degeneration of sexual cells, so commonly observed in the *Ascomycetes*, and particularly the degeneration of the antheridia, leads to the substitution of a conidium for an antheridium, as seen in *Ascobolus carbonarius*. The conidium is modified into the conidiumlike spermatia in the lichens, while some such form as these is further modified into the male cell of the *Laboulbeniales*.

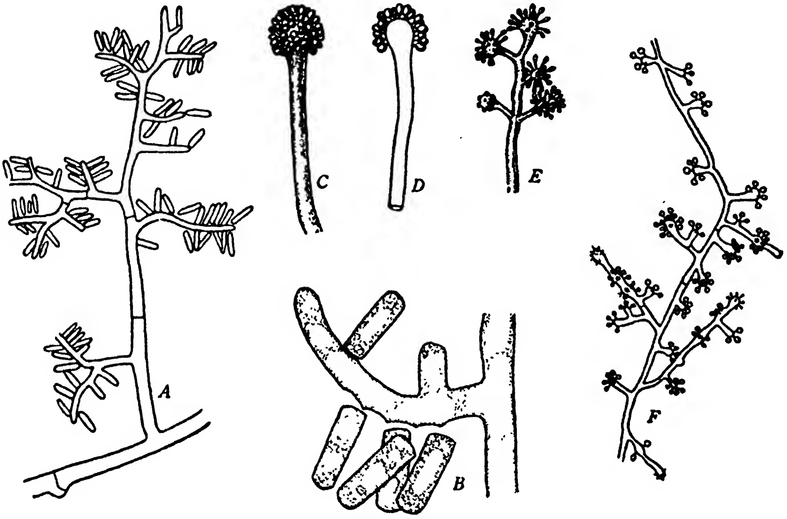


Fig. 716. Conidia of some *Basidiomycetes*

A, B, Corticium alutaceum; C, D, E, Fomes annosus; F, Corticium effuscatum. (After Lyman and Brefeld)

According to the theory that the *Ascomycetes* are derived from the red algae, the *Laboulbeniales* are primitive forms, in which the carpogonium and trichogyne of the red algae have become changed into the ascogonium and trichogyne of the *Ascomycetes*. The male cells of the Laboulbeniales are derived from those of the red algae. In the ascomycetous lichens, regarded as another primitive group, they appear as conidiumlike spermatia. In *Ascobolus carbonarius* they have been replaced by conidia. In typical *Ascomycetes* some such structure develops into the typical antheridium of the *Ascomycetes*. The *Hemiascomycetes*, according to this theory, are degenerate forms.

CLASS *BASIDIOMYCETES*

✓**General characteristics.** The distinguishing characteristic of the *Basidiomycetes* is the basidium, just as the ascus is of the *Ascomycetes*. The basidium is typically a club-shaped structure which bears four spores (Fig. 713). The *Basidiomycetes* include very many and very varied forms. Among them are the largest and most conspicuous of all fungi. They are very familiar as mushrooms and bracket fungi (Figs. 714, 715). The *Basidiomycetes* have become thoroughly adapted to aerial conditions, and offer a striking contrast to the *Oomycetes* in that none of them live in water. The *Basidiomycetes* are similar to the *Ascomycetes* in having septate hyphae.

For convenience the *Basidiomycetes* may be divided into two large groups, the *Eubasidiomycetes* and the *Heterobasidiomycetes*. In the *Eubasidiomycetes* the basidium is a non-septate swollen end of a hypha, from which project slender filaments known as sterigmata, usually four in number, each of which terminates in a single basidiospore (Fig. 713).

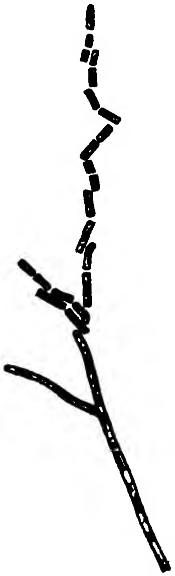


FIG. 717. Oidia formed from hyphae of *Collybia conigena*

After Kniep

In addition to basidiospores, the *Basidiomycetes* may have conidia similar to those of the *Ascomycetes* (Fig. 716). However, conidia are much less important in the *Basidiomycetes* than in the *Ascomycetes*, and in the higher *Basidiomycetes* they play a very unimportant role. To a considerable extent their place is taken by oidia, which are cells formed by the breaking up of hyphae (Fig. 717). The *Basidiomycetes* also reproduce by sprout cells. These are formed as buds, and are constricted off in the same way as are bud cells of yeast.

The *Eubasidiomycetes* can conveniently be again subdivided into two large groups, the *Hymenomycetes* and the *Gasteromycetes*.

Hymenomycetes

General characteristics. The *Hymenomycetes* are characterized by having the basidia borne in a layer, called a hymenium, which is usually compact, and which, when the fruit body is mature, forms an exposed layer (Fig. 713).

Forms of *Hymenomycetes*. There are a great variety of forms among the *Hymenomycetes*. The simplest fruit bodies consist of a loose cobweblike structure which may either form a thin coating over the substratum or take other forms (Fig. 718). In the early stages of such fruit bodies there may be an extensive production of conidia, followed later by basidia with basidiospores.

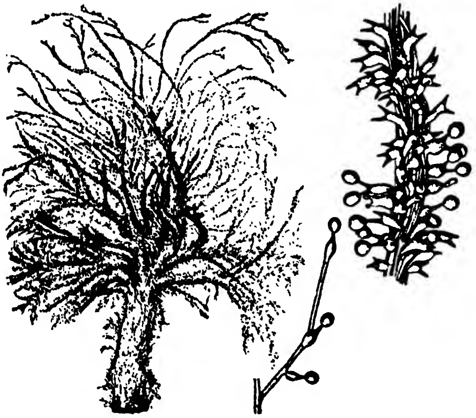


Fig. 718. *Maltruchotia varians*

Left, habit; center, conidia; right, basidia. (After Boulanger)

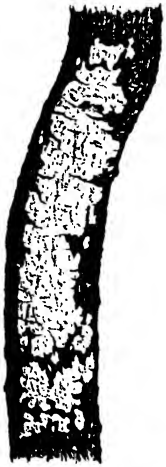


Fig. 719. *Corticium* on a dead branch. (× ½)

The forms with compact fructifications which are regarded as most primitive are those that form smooth coatings on the substratum (Fig. 719) and those (*Clavariaceae*) in which the fruit body has club-shaped branches covered by the hymenium (Fig. 720).

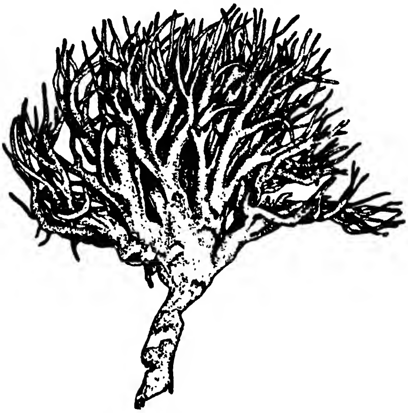


FIG. 720. ***Clavaria***

A basidiomycete in which the hymenium covers the coral-like branches. (× ⅔)

Basidiospores do not fall from the sterigmata, but are shot out a short distance by the turgor of the basidium. With few exceptions the hymenium of the *Hymenomycetes* is on the lower surface. Various factors, such as protection from dust, from rain, or from drying, may be influential in this. It would appear, however, that the production of spores on the lower surface of the fruit body is also connected with the small distance to which the spores are shot when they are discharged from the basidium. This distance in most cases would not be great enough for them to clear the fruit body if the hymenium were on the upper surface.

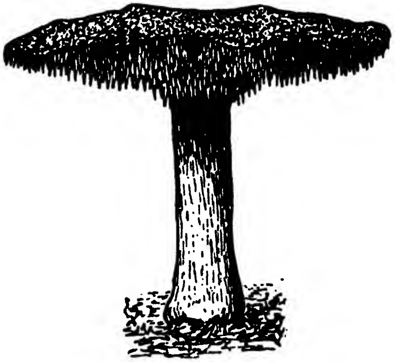


FIG. 721. **A tooth fungus (*Hydnum*)**

The great majority of the *Hymenomycetes* have fruit bodies of three general types, resupinate (Fig. 719), bracket (Figs. 714, 715), and stipitate (Fig. 721). The resupinate type forms a coating which adheres closely to the substratum, such as the under surface of a decaying log or branch. Such forms are, in general, the simplest and most primitive. The resupinate forms grade into others, the edges of which project from the substratum. These, in turn, grade into bracket forms. The most highly developed types are the stipitate. These have a stalk or stipe. In general the simplest of the stipitate forms are those with lateral stipes, and the more advanced those with central stipes.

All of these three types, resupinate, bracket, and stipitate, include forms in which the hymenium is a smooth, continuous, expanded layer (*Thelephoraceae*, Figs. 719, 722); forms in which it covers teeth or toothlike plates (*Hydnaceae*, Figs. 721, 723, 724); and forms in which it lines the inside of pores (*Polyporaceae*, Figs. 714, 715, 725; and *Boletaceae*, Fig. 726).

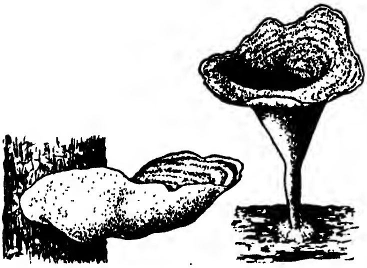


FIG. 722. Bracket and stipitate *Basidiomycetes* with smooth hymenium

Left, *Stereum lobatum* (× ½); right, *Stereum affine* (× 1½)

Forms with spines and pores probably developed from forms with smooth surfaces. Between the typical smooth surface of the smooth forms and the deep pores of the *Polyporales* we find intermediate forms with folded surfaces and others with shallow pores.

The most advanced of the *Hymenomycetes* are the *Agaricaceae*, or gill fungi (Fig. 727). In these the hymenium covers radiating hanging plates or gills. The two most important families of the *Hymenomycetes* are the *Polyporaceae* and the *Agaricaceae*.

Primary hyphae. The basidiospores of the *Hymenomycetes* usually germinate to produce either a mycelium with uninucleate cells or one in which the cells are at first multinucleate but become uninucleate by septation. These hyphae are known as the first, or primary, hyphae. It is the uninucleate mycelium that usually gives rise to such reproductive structures as oidia (Fig. 717) or conidia, if these are present. Neither these uninucleate hyphae nor any other type of hyphae are known to produce special sexual cells.

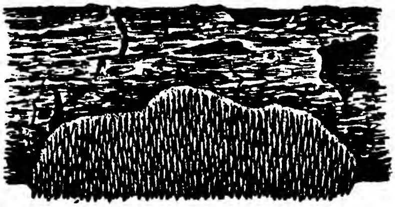


FIG. 723. A resupinate form of *Hydnum*, a tooth fungus growing on a dead branch. (× 1)

Secondary hyphae. In the *Hymenomycetes*, in spite of the fact that there are no sexual organs, the uninucleate hyphae are usually sexually differentiated. There are two strains which correspond to the + and — strains of the molds, and unless there is a union of these two strains no fruit bodies are formed. When a cell from a + and one from a — hypha meet, two cells unite and the nuclei form a dicaryon of a binucleate cell (Fig. 728). This gives rise to a mycelium with binucleate cells. The nuclei composing a dicaryon divide together by conjugate division (Fig. 729). There are various complications, but it seems to be typical for both nuclear and cell divisions to take place in much the same way as in the later or hook stages of the ascogenous hyphae.

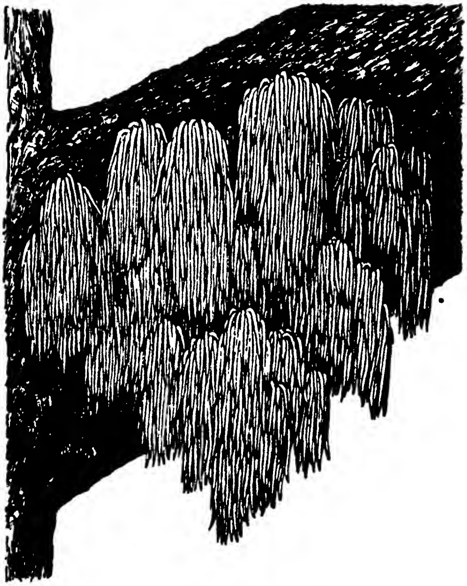


FIG. 724. A bracket form of *Hydnum*. (× ½)

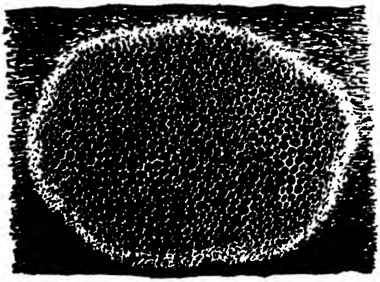


FIG. 725. *Poria*, a resupinate pore fungus. (× 3)

This typical process is as follows (Fig. 729): Before the nuclei begin to divide, a hooklike projection known as a clamp grows out from the hypha between the two nuclei and curves toward the base of the cell. The nuclei migrate so that one is partly within the projection and the other near its base. In dividing, the nucleus which is partly within the clamp forms a daughter nucleus toward the tip of the main cell and one in the clamp. One of the daughter nuclei of the other nucleus is above the clamp and the other below it. A cell wall is then formed across the base of the clamp, and another across the main cell. This results in a binucleate terminal cell, a uninucleate clamp cell, and a uninucleate basal cell. Usually the tip of the clamp cell fuses with the basal cell and its nucleus enters the basal cell so that the latter again becomes binucleate. The result is that instead of one binucleate cell there are two binucleate cells, and that the two nuclei in a cell are not sisters but are the result of conjugate division.

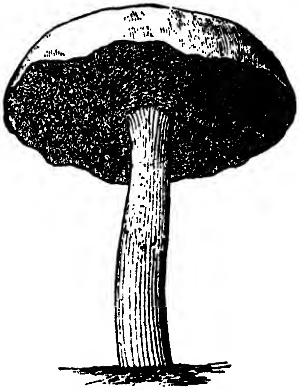


Fig. 726. ***Boletus*, a stipitate pore fungus. (× ½)**

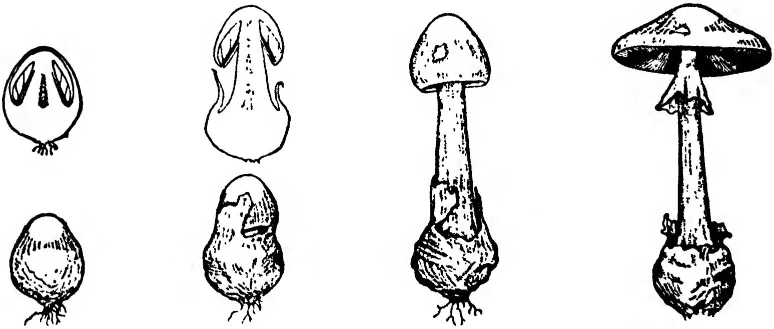


Fig. 727. Development of a gill fungus, the deadly amanita (*Amanita phalloides*)

Redrawn after Longyear

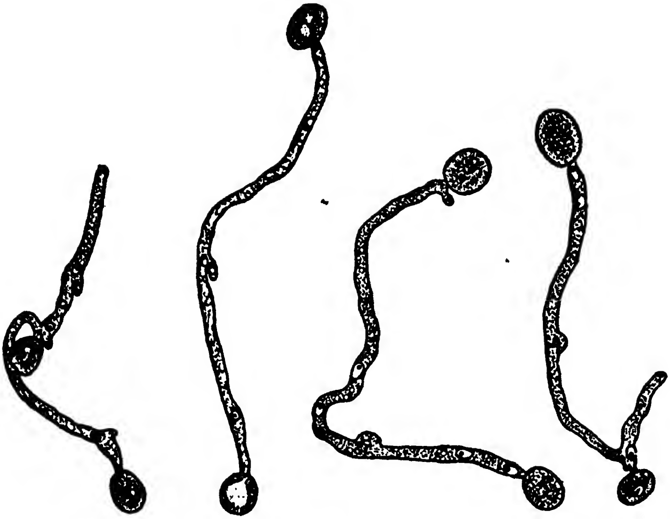


Fig. 728. *Corticium serum*

Conjugation of hyphae produced by germinating spores. Note clamp connections. (After Lehfeldt)

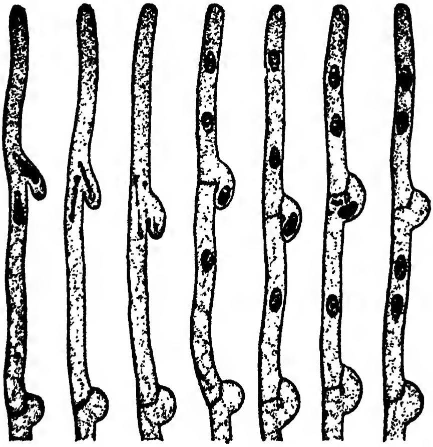


Fig. 729. Semidiagrammatic representation of conjugate division and formation of clamp connections in the hyphae of *Basidiomycetes*

Based on figures by Kniep

A terminal cell of a hypha with a hooklike clamp is apparently a slight modification of a hook of the *Ascomycetes.* The clamp cell of the *Basidiomycetes* appears to correspond to the ultimate cell of the ascus hook, the terminal binucleate cell to the binucleate cell of the hook, and the uninucleate basal cell to the basal (antepenultimate) cell of the ascus hook. In both cases the basal cell may become binucleate by the migration of a nucleus from the tip of the hook.

Tertiary hyphae. When the secondary hyphae have stored sufficient food material and the conditions are otherwise favorable, the mycelium begins to form the fruit body. This process is not initiated by any sexual process, as the cells of the hyphae are already binucleate and this condition continues until the formation of the basidia. In the formation of the fruit body the hyphae become differentiated for the various functions which they are to perform, and are known as tertiary hyphae.

Some of the hyphae may be differentiated into conduction cells by enlarging and losing their cross walls. In function these are like the sieve tubes of the flowering plants. Other hyphae may develop thick walls and even become woody, and thus serve as strengthening or protective hyphae. These take the place of sclerenchyma in higher plants. In many genera some of the hyphae become modified into latex ducts which, superficially, correspond to the latex ducts of angiosperms.

Formation of basidium. The basidium is formed by the enlargement of a terminal cell (Fig. 730). This cell may result from nuclear and cell divisions of the type previously described (Fig. 730), but this method is not universal. As in the case of ordinary hyphae, the nuclei may divide without clamp connections. A tip cell which gives rise to a basidium is naturally binucleate. In the basidium the two nuclei fuse to form the mother nucleus of the basidium (Figs. 730, 731). The fusion nucleus divides to form four nuclei. Four slender projections, sterigmata, grow from the tip of the basidium, and the tip of each of these enlarges to form a basidiospore. The four nuclei of the basidium then migrate singly through the sterigmata into the basidiospores (Fig. 731).

Variations in life history. Variations from the above-described life history include species which are homothallic and cases in which the nuclei of a dicaryon divide conjugatively in the hyphae without the formation of clamp connections. In one interesting case a basidium produces two

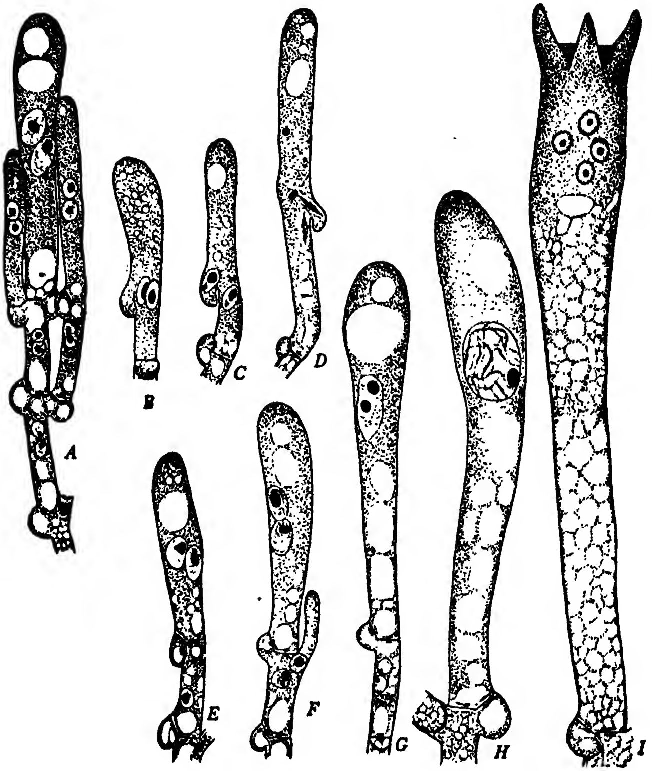


Fig. 730. Formation of basidium of *Armillaria mucida*

A, end of a hypha, bearing in the center a young basidium and to the left and right hyphae which will also give rise to basidia; *B*, binucleate terminal cell showing the beginning of clamp formation; *C*, one nucleus has migrated into the clamp; *D*, conjugate division of the two nuclei, one division spindle being partly in the clamp; *E*, nuclear division has been completed and walls have been formed so as to produce a uninucleate basal cell, a binucleate basidium, and a uninucleate clamp cell; *F*, the clamp cell has fused with the basal cell, its nucleus has migrated into the basal cell, and the basal cell is sending out another hypha; *G*, the two nuclei in the basidium have fused to form the primary nucleus of the basidium, in which the nucleoli are prominent; *H*, a further stage in the development of the basidium and its nucleus; *I*, the primary nucleus of the basidium has divided to form four nuclei which will migrate into the four spores; at the tip of the basidium four projections which will give rise to basidiospores are already formed. (After Kniep)

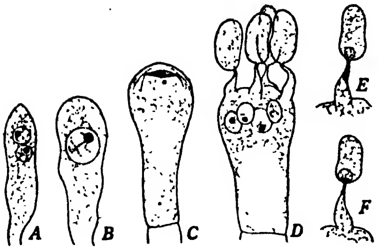


FIG. 731. **Formation of basidiospores by basidium**

A, binucleate basidium. *B*, two nuclei have fused to form primary nucleus of basidium. *C*, primary nucleus of basidium is dividing. *D*, basidium contains four nuclei formed by the division of the primary nucleus; the sterigmata and basidiospores are already formed. *E*, *F*, migration of nucleus into basidiospore. (After Ruhland)

basidiospores, each of which receives two nuclei from the basidium. These two nuclei form a dicaryon. The first division in the hypha which grows from the germinating spore is conjugate and with the formation of a clamp connection (Fig. 732). Here the dicaryon condition persists throughout the whole life of the plant except for the brief phase in the basidium after the nuclei of the dicaryon have fused to form the nucleus of the basidium and before the division of this has produced the nuclei for the basidiospores.

Origin of *Basidiomycetes*. The *Basidiomycetes* are generally regarded as being descended from the *Ascomycetes*. The great similarity between the secondary hyphae of the *Basidiomycetes* and the ascogenous hyphae of the *Ascomycetes* is strong evidence in support of this view. In many groups of *Ascomycetes* there is a progressive degeneration of the sexual cells until the ascogenous hyphae arise from vegetative cells. In the *Eubasidiomycetes* the absence of specially differentiated sexual cells has become universal and there is a union of vegetative cells.

In the *Ascomycetes* the stage in which there are dicaryons dividing by conjugate division is confined to the ascogenous hyphae, which are reproductive in function. In the *Basidiomycetes* this phase has been lengthened to include the greater part of the vegetative development.

In the *Basidiomycetes* there is reproduction by conidia similar to that in the *Ascomycetes*.

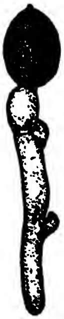


FIG. 732. Binucleate basidiospore of *Galera tenera f. bispora* germinating

The two nuclei form a dicaryon. Notice early appearance of clamp connections. (× 800). After Sass

Along with the development of the importance of the secondary mycelium and a great efficiency in basidiospore production there has been a decrease in the importance of conidia. These are confined largely to the primary mycelium.

The basidium with its basidiospores is regarded as a modified ascus. The cell which becomes the basidium may be formed in a way which is very similar indeed to the formation of the cell which becomes an ascus in one of the typical *Ascomycetes*. Usually the nucleus of an ascus divides into eight nuclei and there are eight ascospores. In the basidium the nucleus usually divides into four and there are four basidiospores. However, in some *Basidiomycetes* which may be regarded as primitive, and which otherwise have a typical basidium, the nucleus of the basidium divides into eight and there are usually eight basidiospores.

The striking difference between the ascus and the basidium is the fact that ascospores are formed inside the ascus and basidiospores on the outside of the basidium. This is thought to be due to a process similar to that by which a sporangium of one of the *Zygomycetes*, such as *Rhizopus*, has been converted into a group of conidia on the rounded head of a conidiophore.

Polyporaceae. In the *Polyporaceae*, or pore fungi, the hymenium is the lining of pores, which in many cases are long and narrow (Figs. 714, 715). The pores hang down vertically, and the force of the discharge of the spores is just great enough to carry them to the middle of the tube so that they may fall freely. After falling from the pore they may be caught by the wind, and, owing to their lightness, be carried to considerable distances. Some of the *Polyporaceae* are small; others are very large. They are mostly leathery, corky, or woody. Some have perennial fruit bodies and each year add a new and wider layer of pores over the lower surface of these (Figs. 714, 715). The number of spores produced by a large fruit body may be enormous. A large one may produce as many as one hundred billion spores per annum; and spores may be discharged at the rate of at least a million a minute for several hours or days.

Agaricaceae. The *Agaricaceae* are often called gill fungi because the hymenium covers the surface of thin plates or gills which hang down from the pileus and radiate out from the stalk. Most of the *Agaricaceae* have a central stipe (Fig. 727). The name "mushroom" is variously used for all *Agaricaceae* or for the edible *Agari-*

caceae. *Agaricaceae* usually grow saprophytically on decaying vegetable matter in the soil, but some are parasitic on trees.

In the young stages of the *Agaricaceae* the edge of the pileus is joined to the stipe. In many this connection becomes a fairly firm thin sheet which is ruptured as the mushroom expands, and remains as a veil, or annulus, attached to the stalk (Fig. 727, right). This is true in the common cultivated or field mushroom, *Agaricus campestris*. In the young stage of many mushrooms the unexpanded pileus and stipe are enclosed in a stout covering through which the mushroom, in expanding, breaks; and this persists as a cup or volva around the base of the stipe (Fig. 727).

Many of the mushrooms are edible and are delicious articles of food. Others are very poisonous; this is particularly true of various species of *Amanita*, a genus which is characterized by having both veil and volva (Fig. 727). There are also species of mushrooms which make people sick but which are seldom, if ever, fatal. Still others appear to be poisonous to some but not all people. As poisonous and edible species may be found in the same genus, there is no way of distinguishing poisonous and edible mushrooms except by knowing the individual species.

Gasteromycetes

General characteristics. The *Gasteromycetes* are distinguished from the *Hymenomycetes* by the fact that in them the hymenium is found on irregular plates of tissue which anastomose to form a system of cavities (Fig. 733). The fertile tissue is surrounded by a covering of sterile tissue which does not open until the spores are mature.

It is characteristic of the basidiospores of the *Gasteromycetes* to have two nuclei. On germination the basidiospore gives rise to a mycelium with binucleate cells in which the nuclei form a dicaryon and divide from the first by conjugate division. Most of the *Hymenomycetes* have uninucleate basidiospores which give rise to a primary mycelium with uninucleate cells. Some of the *Hymenomycetes* are like the *Gasteromycetes* in having binucleate basidiospores which germinate to produce a mycelium with binucleate cells. In these and in the *Gasteromycetes*, the primary mycelium, characteristic of the *Hymenomycetes*, seems to be omitted.

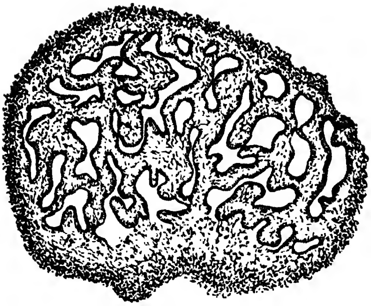


Fig. 733. Section of *Hymenogaster decorus*, one of the tuberous *Gasteromycetes*

The hymenium lines the cavities. (× 18). After Rehsteiner

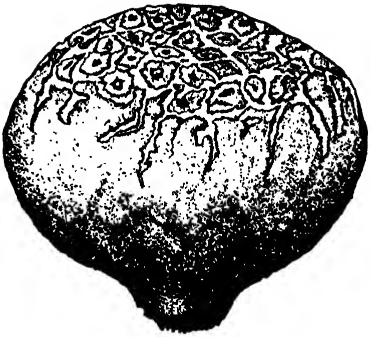


Fig. 734. Puffball (*Lycoperdon cyathiforme*)

Redrawn after Farlow. (×½)

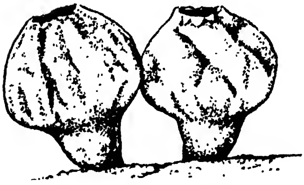


Fig. 735. Puffballs which have opened at the top. (× 1⅕)

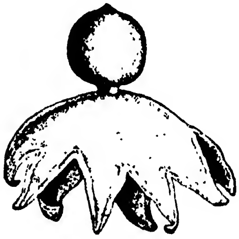


Fig. 736. *Geaster limbatus*

The sterile covering splits into two parts, one of which surrounds the spore mass while the other curves back, forming a star-shaped structure. (× ½)

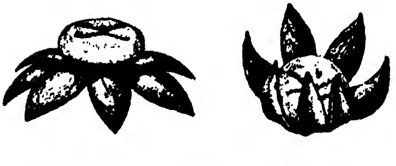


Fig. 737. *Geaster hygrometricus*

Left, position when moist; right, position when dry. (× ½)

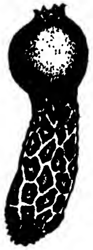


Fig. 738. *Calostoma fusca*

The upper portion contains the spores; the lower part is the stalk. (× ½). After Cooke

Types of *Gasteromycetes*. The *Gasteromycetes* include a number of very curious and interesting forms. Among these are the puffballs (Figs. 734, 735). When the puffball is mature, it has a tough outer covering within which the spores occur in a powdery mass. These fungi get their name from the fact that spores puff out in clouds when pressure is applied to their sides. A geaster, or earthstar, looks like a puffball arising from the center of a star-shaped cup (Figs. 736, 737). The star is formed by the splitting and spreading of the outer layer of the sterile covering of the fruit body. In the birds'-nest fungi (Figs. 739–741) each fertile chamber is surrounded by a dense region (Figs. 740, 741); when the entire fruit body opens up, the outer part becomes the nest while the fertile chambers with their hard coverings become the eggs. The stinkhorns are curiously formed and evil-smelling fungi (Figs. 742, 743). In them the fertile tissue changes to a sticky ill-smelling slimy mass. This attracts flies which scatter the spores.

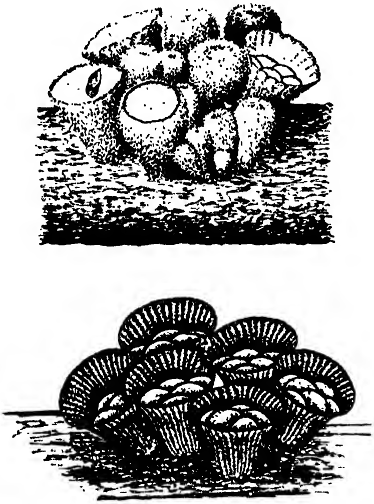


FIG. 739. *Cyathus striatus*

Above, various stages in development. Below, a group of mature fruit bodies; the basidiospores are within the "eggs"

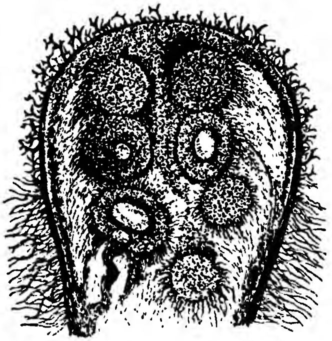


FIG. 740. Longitudinal section of unopened bird's-nest fungus, *Crucibulum vulgare*

Note the dense outer region, which will form the nest, and the dense structures within, which will become the "eggs." (After De Bary)

Heterobasidiomycetes

The *Heterobasidiomycetes* include those forms in which the basidium is septate. There are two types of such basidia: one in which the septa are longitudinal so that, typically, the basidium is divided into four cells which are more or less parallel (Fig. 746), and another in which the septa are transverse so that the basidium is divided into a row of four cells (Fig. 746).

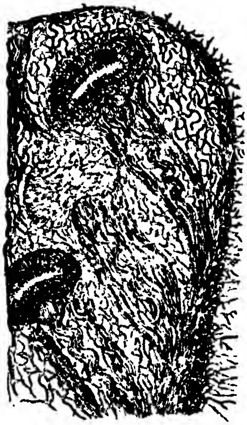


Fig. 741. ***Crucibulum vulgare***

Highly magnified view of portion of a section such as is seen in Fig. 740. Note the hymenium inside the "eggs." (After De Bary)

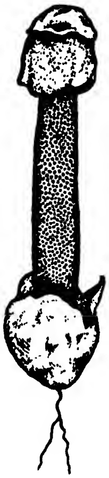


Fig. 742. ***Ithyphallus*, a stinkhorn fungus. (× ½)**

Basidiomycetes with longitudinal septate basidia are included in one order, the *Tremellales*. Those with transverse septate basidia are divided into three orders: the *Auriculariales*, the *Uredinales*, and the *Ustilaginales*.

Tremellales

The best-known of the *Tremellales* are the trembling fungi of the genus *Tremella* (Fig. 747). These grow on decaying wood and form irregularly-shaped fruit bodies which, when moist, have a gelatinous consistency. They are variously colored and have a somewhat translucent appearance. In the *Tremellales* there is a series from very simple forms to those which, like *Tremella*, have definite fruit bodies. The basidium is always longitudinally septate, and typically bears four spores (Fig. 748).

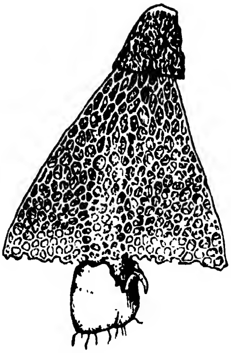


Fig. 743. *Dictyophallus*, a stinkhorn fungus

The ripe spores occur in a sticky mass on the cap, which is above the veil. (× ½)

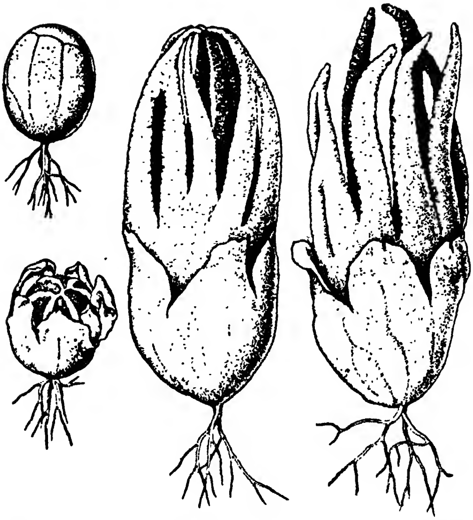


Fig. 744. Opening of the fruit body of *Anthurus brownii*, one of the *Gasteromycetes*

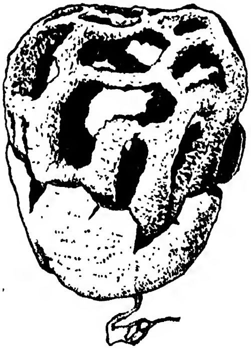


Fig. 745. *Clathrus cancellatus*

From a photograph by Lloyd

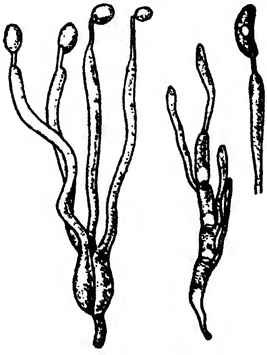


Fig. 746. Basidia of *Tremella* (left) and *Auricularia* (right)

After Brefeld from Tavel

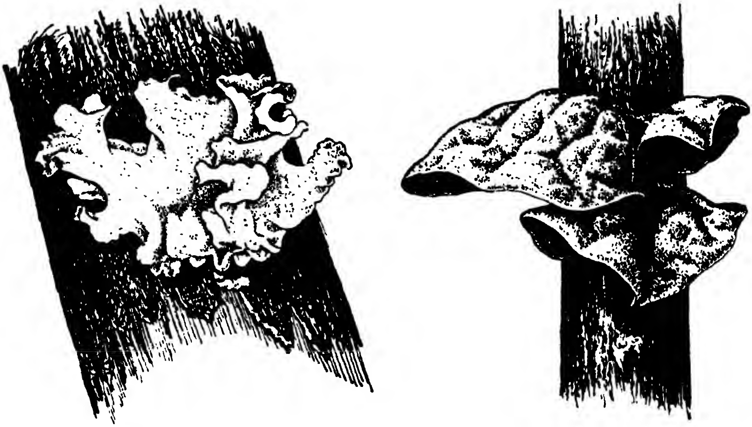


Fig. 747. *Tremella* (left) of the order *Tremellales*, and *Auricularia* (right) of the order *Auriculariales*

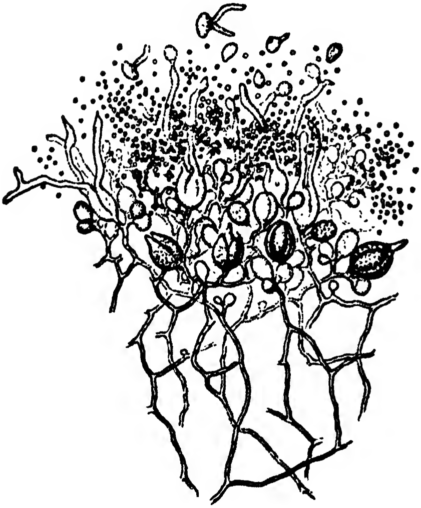


Fig. 748. *Tremella mesenterica*

Portion of hymenium showing basidia with basidiospores and also production of conidia. (After Tulasne)

Auriculariales

The best-known of the *Auriculariales* is *Auricularia*, the ear fungus, which grows on decaying wood (Fig. 747). The fruit bodies have somewhat the shape of an ear; hence the name. They are very variable in size, dark brown in color, gelatinous when moist, and leathery when dry. The basidia are borne in a hymenium. They are transversely septate into four cells, each of which, typically, gives rise to a filament terminating in a basidiospore (Fig. 746). *Auricularia* is edible, and when cooked has a good flavor and consistency. It is much used and highly prized by the Chinese, and is often an important constituent of chop suey. In the *Auriculariales* we again find a series of forms leading from very simple indefinite fructifications to the regular fruit bodies of *Auricularia*. In some of them there are clamp connections which indicate a relationship to the *Eubasidiomycetes*.

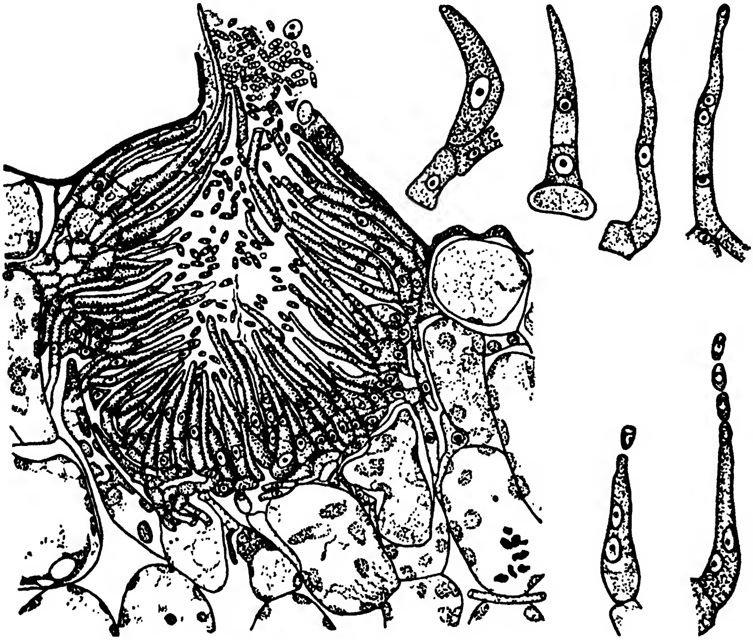


FIG. 749. ***Puccinia graminis***

Left, section of a pycnium (× 600); right, development of spermatia. After Allen

Uredinales (Rust Fungi)

General characteristics. The rusts are important fungi because they cause a considerable number of very serious plant diseases. They are parasitic on higher plants. One of the best-known of the rusts is *Puccinia graminis*, which does great damage to wheat. The rusts have a very complicated life history, and many, like *Puccinia graminis*, produce five kinds of reproductive cells. Some have a shorter life history. In *Puccinia graminis*, as in many others, two hosts are necessary for the completion of the life history.

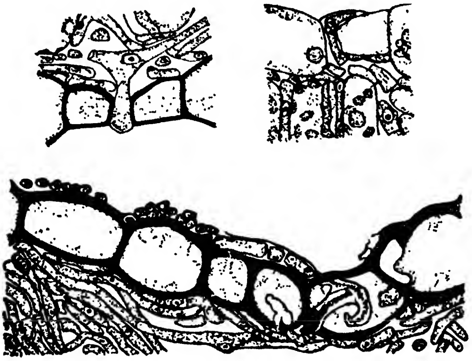


Fig. 750. Receptive hyphae of *Puccinia*

Upper left, a hypha of *Puccinia triticina* in a stoma; upper right, a hypha of *Puccinia coronata* which has grown out between epidermal cells and below the cuticle; below, hypha of *Puccinia coronata* in contact with spermatia. After Allen

Spermatia. In the spring, basidiospores of *Puccinia graminis* germinate and infect the leaves of the barberry bush. A spore produces a hypha which enters a leaf and gives rise to a mycelium. After a few days the mycelium produces flasklike structures, known as pycnia (Figs. 749, 751), which project from the upper surface of the leaf. Within the pycnia are a large number of hyphae which point toward the opening, and from the ends of which conidium-like bodies, called spermatia or pycnidiospores, are constricted off successively (Fig. 749). For a long time these were generally regarded as functionless, although some authorities believed that they were degenerate male cells. Recently it has been proved that in *Puccinia graminis* and some other rusts they do act as male cells.

Aeciospores. In *Puccinia graminis* the primary hyphae, which produce spermatia, have uninucleate cells. A spermatium comes in contact with such a uninucleate cell and fuses with it, with the

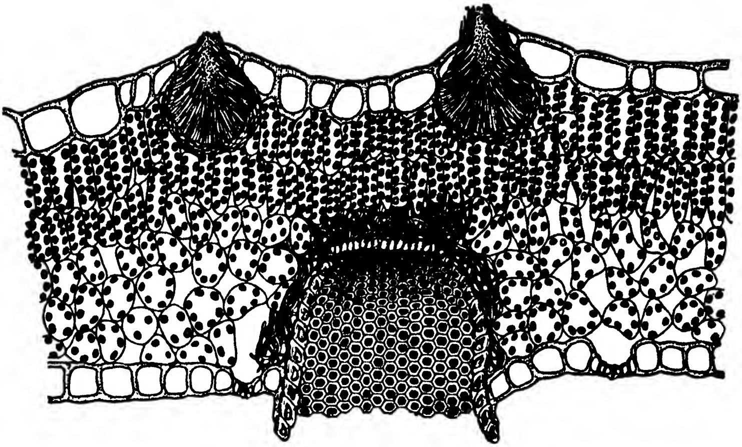


Fig. 751. Leaf infected with aeciospore stage of rust

Above are two pycnia, and below an aecium. (× 165)

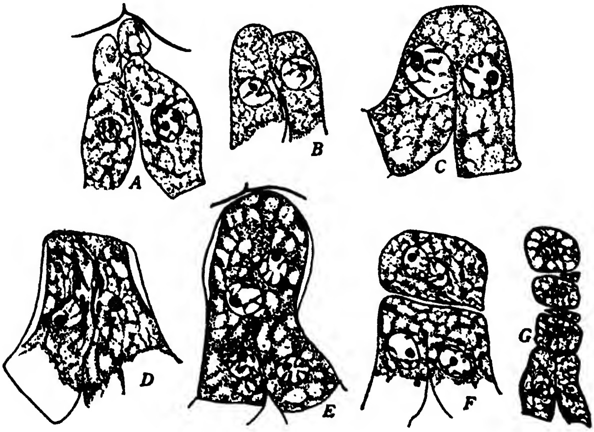


Fig. 752. Cell fusions in a rust, *Phragmidium speciosum*

A, ends of two hyphae with sterile cells at the tips and large fertile cells below; *B*, *C*, fusion of fertile cells; *D*, conjugate division of the two nuclei; *E*, four nuclei formed as a result of conjugate division; *F*, aeciospore mother cell cut off; *G*, later stage showing row of aeciospores and intercalary cells. (After Christman) result that there is produced a mycelium in which the cells are predominantly binucleate, although there is some irregularity and there may be more than two nuclei in a cell. In some species of rusts there are hyphae which grow to the surface of the leaf of the host and come in contact with the spermatia (Fig. 750).

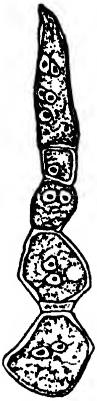


Fig. 753. Aeciospore chain of *Puccinia graminis*

From top to bottom, the basal cell, three spore mother cells, an intercalary cell, and an aeciospore. Not all nuclei are shown. (From Allen)

We have noted that in various groups of fungi there are heterothallic species. *Puccinia graminis* is heterothallic. The + and − strains cannot be distinguished except by the fact that a + spermatium will only fertilize a − mycelium, while a − spermatium will fertilize a + mycelium.

After the mycelium is fertilized by fusion with a spermatium, it produces aecia, which are cup-shaped structures, in each of which a very large number of aeciospores are developed (Fig. 751). In some cases the binucleate condition has been said to be the result of the fusion of two cells at the base of the aecium (Fig. 752). It may be that in the same species cells may become binucleate by both of the methods described above. The nuclei in the binucleate or multinucleate cells at the base of

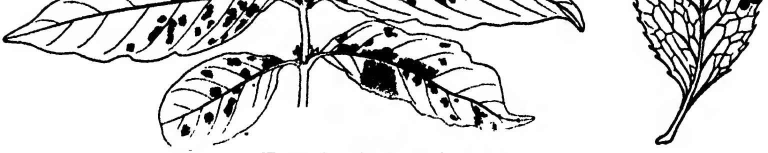


Fig. 754. Stages of rusts

Left, coffee infected with urediniospore stage of coffee rust (*Hemileia vastatrix*) (× ⅓); right, aeciospore stage of wheat rust (*Puccinia graminis*) on barberry leaf (× 1)

the aecium divide by conjugate division, and the basal cells of the aecium produce chains of cells, each cell of which is known as a spore mother cell (Figs. 752, 753). The nuclei of the spore mother cell divide by conjugate division, and the cell divides to form a large spore cell and a small intercalary cell (Figs. 752, 753). The intercalary cells disintegrate and disappear and thus separate the aeciospores from each other. When seen with the unaided eye, the aecia of *Puccinia graminis* appear as small raised orange-colored patches on the surface of the barberry leaf (Fig. 754).

Urediniospores. The aeciospores are capable of germinating at once and producing a mycelium that can infect a susceptible host. The aeciospores of *Puccinia graminis* cannot infect the barberry bush, but can infect a wheat plant, in which they produce a mycelium. This mycelium produces spores which are known as urediniospores. In *Puccinia graminis* these occur in

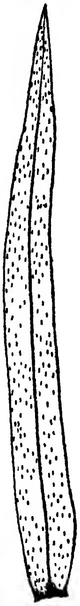


Fig. 755. Urediniospore stage of wheat rust (*Puccinia graminis*). (× ½)

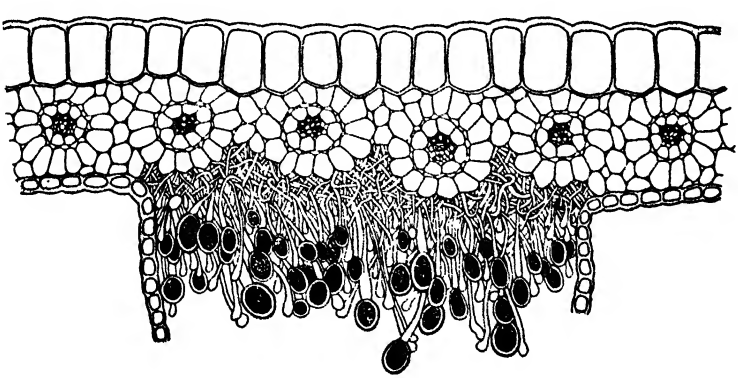


Fig. 756. Urediniospore stage of a rust

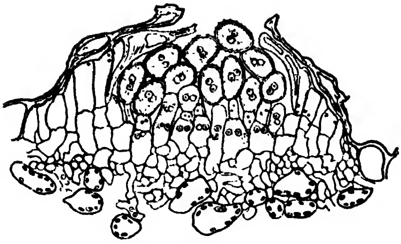


Fig. 757. Section through small group of urediniospores of *Cronartium ribicola*

Note that the spores, stalk cells, and basal cells are all binucleate. (× 250). After Crolley

grayish-brown or rust-colored patches on the stems and leaves of the wheat plant (Fig. 755). Urediniospores of *Puccinia graminis* and other species (Figs. 756, 757) are formed singly on fairly long stalks. The urediniospores of *Puccinia graminis* are capable of germinating on wheat plants; so during the growing season they may cause a widespread infection.

Teliospores. Later in the season, after the wheat plant matures, the same mycelium which produced urediniospores produces another type of spore known as a teliospore. The teliospore of *Puccinia graminis* and various other species of rusts (Figs. 758, 759), is a two-celled spore with thick walls. In *Puccinia graminis* it is a winter spore: it persists throughout the winter and germinates the following spring.

Basidiospores. In the spring, when moisture and temperature conditions are favorable, each cell of the teliospore germinates by sending out a hypha which becomes a basidium that is typically divided into four cells by transverse septa (Fig. 760). Each of these cells gives rise to a basidiospore. In *Puccinia graminis* these cannot infect the wheat plant but are capable of producing a mycelium in the leaves of the barberry.

Nuclear history. In the rusts two nuclei become associated as a dicaryon in the mycelium which gives rise to the aecia. This condition persists in the aeciospores and throughout the mycelia which produce urediniospores and teliospores. Each of the cells of the teliospores of *Puccinia graminis* contains a di-

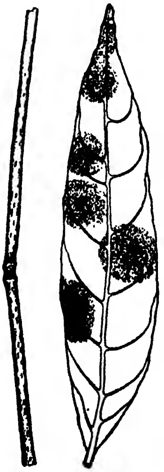


Fig. 758. Teliospore stages of rusts

Left, wheat rust (*Puccinia graminis*) (× ½); on the right, *Puccinia thwaitesii* on a dicotyledon (× ⅔) caryon. In each of these cells the nuclei fuse. Reduction in the number of chromosomes occurs when this fusion nucleus divides to give rise to the nuclei of the basidiospores. In the rusts there is, then, as in the *Hymenomycetes,* a short period in which the cells are uninucleate, followed by a dicaryon condition which persists throughout the greater part of the life cycle.

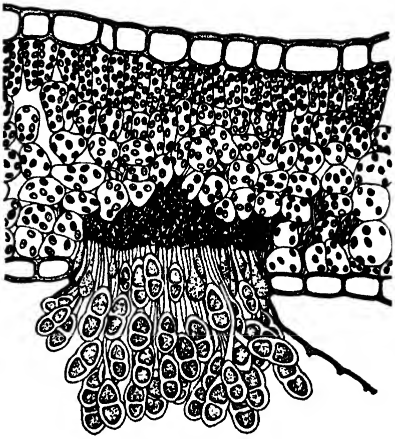


Fig. 759. Leaf infected with teliospore stage of a rust. (× 140)

As the complete life history of *Puccinia graminis* requires two hosts, the wheat plant and the barberry bush, the wheat rust can be controlled to a considerable extent by eradicating barberry bushes. In some cases this method has been highly successful. But it is not always possible to eradicate wheat rust in this way, as when conditions are not too severe some urediniospores may survive the winter and cause infections in wheat plants the next spring.

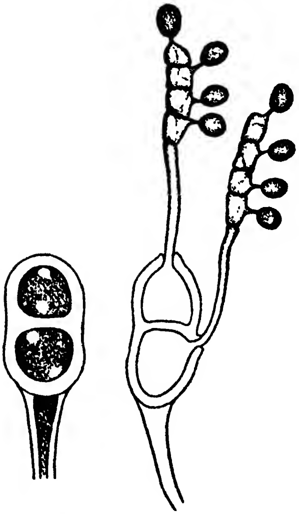


Fig. 760. Teliospore (left) and germination of teliospore (right) with production of basidiospores (somewhat diagrammatic). (× 445)

The white pine blister rust is another example of a serious plant disease with two hosts. In the case of this fungus the spermatia and aecia are formed on some of the white pines and the urediniospores and teliospores on currants or gooseberries. This disease is very destructive to susceptible pines and particularly to young plants.

Where the whole life of the rust is spent on one host, it may be exceedingly difficult to eradicate it. The coffee rust has destroyed the coffee industry in many parts of the Far East, as the rust grows on the coffee throughout the year and the best coffee is very susceptible to it.

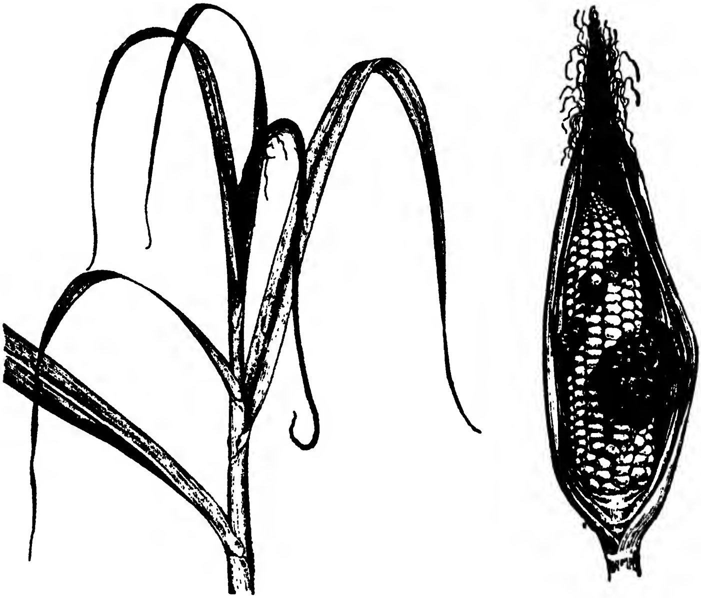


FIG. 761. The *Ustilaginales*, or smuts

Left, tip of sugar-cane plant infected by smut (*Ustilago sacchari*) (× $\frac{3}{20}$); the black whiplike tip is little more than a mass of spores. Right, ear of corn showing swellings produced by smut (*Ustilago zeae*) (× $\frac{3}{10}$)

Ustilaginales

General characteristics. The *Ustilaginales*, or smuts, like the *Uredinales*, are very important on account of the fact that a considerable number of them give rise to plant diseases of serious economic importance. They are characterized by producing a great mass of black spores which give the infected part a burned or charred appearance (Fig. 761). When the infected material is shaken, the spores often scatter as great clouds of dust.

The structure and life history is comparatively simple. The hyphae produce an abundant mycelium in the host. In the majority of cases the cells of this mycelium become divided up into cells which are transformed into spores (Fig. 762). In no case is there a definite fruit body (Fig. 763). Clamp connections are known in the smuts (Fig. 762) and emphasize their relationship to other *Basidiomycetes*.

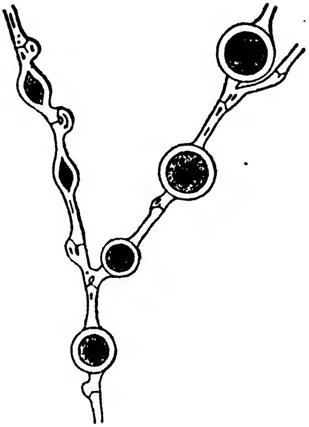


Fig. 762. Formation of spores from mycelium of *Ustilago vuijckii*

Note clamp connections. (After Seyfert)

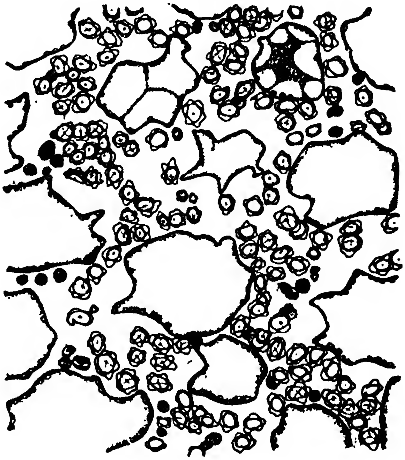


Fig. 763. Spores of a smut (*Tuburcinia*) in tissue of onion leaf

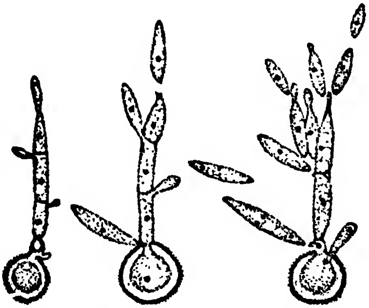


Fig. 764. Promycelium and sprout cells of *Ustilago zeae*. (× 830)

After Hanna

Corn smut. The corn smut, *Ustilago zeae*, is common and well-known and will serve as an example of smuts. The spore germinates in a way which is rather similar to the germination of the teliospores of rusts (Fig. 764). In germinating it sends out a small hypha which is often called a promycelium. This, typically, divides into four cells. These four cells correspond to the four cells of the rust basidium. In smuts each of these cells may give rise to a single sporelike cell corresponding to a basidiospore and variously called a sporidium or sprout cell (Fig. 765), but there is great irregularity, and often many sprout cells are budded off from the mycelium (Fig. 766). In corn smut the sprout cells may infect any part of the corn plant and produce a mycelium. Cells of this mycelium conjugate within the host, the nuclei of the fusing cells

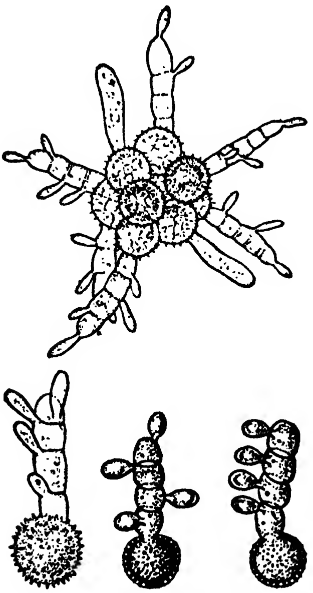


Fig. 765. Promycelium and sprout cells of *Ustilago*

Above and lower left, *Ustilago receptaculorum*; lower center and right, *Ustilago marginalis*. (After Tulasne and Brefeld)

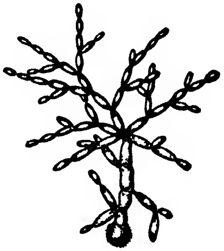


Fig. 766. Promycelium of *Ustilago zeae* with many sprout cells

After Brefeld

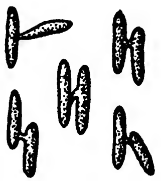


Fig. 767. Fusion of sprout cells of *Ustilago receptaculorum*

After Brefeld

forming a dicaryon. The result is a binucleate mycelium in which the nuclei divide by conjugate division. It is this mycelium that divides up to form the spores. During the development of the spores the two nuclei of the dicaryon fuse. Reduction in the number of chromosomes takes place during the first divisions of the fusion nucleus.

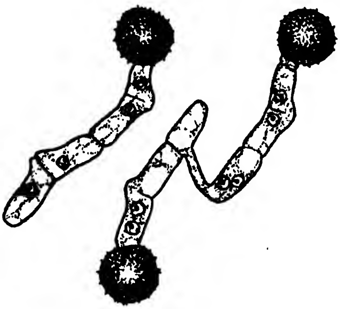


FIG. 768. *Ustilago carbo*

Left, fusion of cells in same promycelium; right, fusion of cells in same promycelium, also fusion of cells of different promycelia. (× 835). After Rawitscher

In most of the smuts closely related to *Ustilago zeae*, two sprout cells unite outside the host either directly or through a conjugating tube to form a binucleate cell (Fig. 767). Sometimes two cells of the promycelium fuse to form a binucleate cell (Fig. 768). The binucleate cells give rise to cells capable of infecting a host. In some rusts, often called stinking rusts (of which the wheat rust, *Tilletia tritici*, is an example), the spores germinate in a different way from those of the corn smut. They send out a short tube at the end of which a number of basidiospores, often four or eight, are formed. These unite in pairs either while they are attached (Fig. 769) or after they have fallen away. The fusion cell gives rise to a mycelium which forms conidia that infect the host. The nuclear history in such cases is much like that of the other type of smuts.

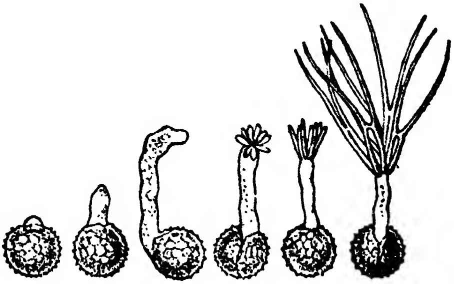


FIG. 769. The germination of spore of *Tilletia caries* to form basidiospores

The last figure shows fusion of basidiospores in pairs while still attached. (× 300). After Tulasne

In most of the worst smuts the spores adhere to the seed of the host and infect the young seedlings. Such smuts can be controlled by treating the seeds with suitable poisons. Other smuts may infect plants later in life.

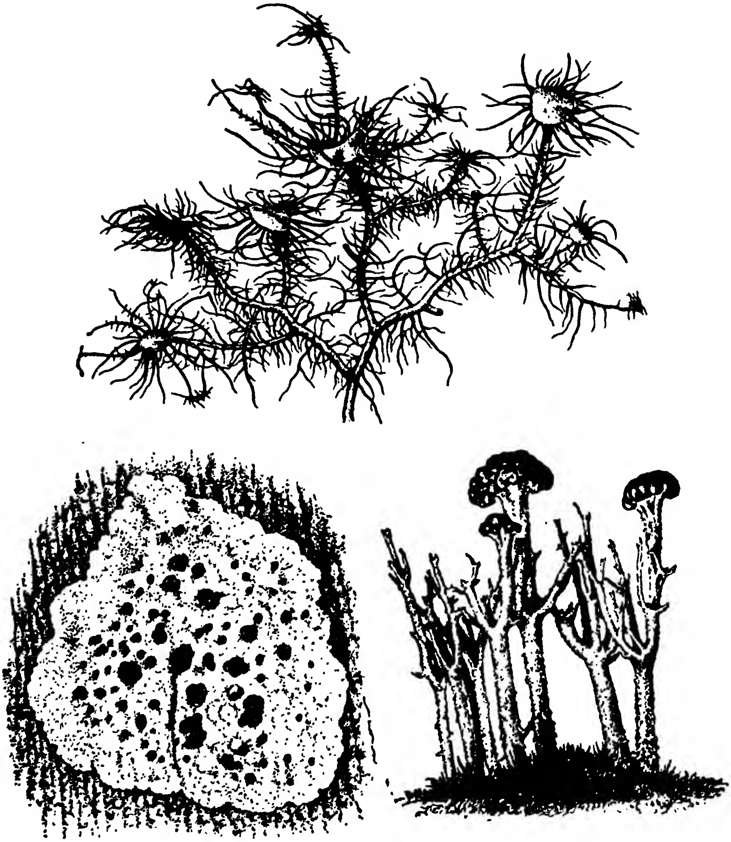


Fig. 770. Three forms of lichens

Above, *Usnea barbata*, a branched epiphytic form; the circular discs are the fruit bodies. Lower left, *Haematomma puniceum*, a crustaceous form; the dark cup-shaped structures are the fruit bodies. Lower right, *Cladonia furcata*, an erect terrestrial form; the hymenium covers the rounded knobs

Some infect flowers, and through these the stems and plants which develop from them. The corn smut can infect any part of the corn plant. In this case the best method of control is the removal and burning of infected parts before spores are formed, or a rotation of crops.

Lichens

Lichens (Figs. 770, 771, 772) are especially interesting plants because in every case a lichen is composed of two very different kinds of plants, an alga and a fungus. The fungus and alga are so thoroughly suited for growth together that different combinations form definite and distinct species. The alga may belong to either the *Chlorophyta* or the *Cyanophyceae*. The fungus composes the larger part of the lichen, while the algae are enclosed between fungus hyphae; usually they form a layer near the upper surface of the lichen (Fig. 773). Most lichens are greenish-gray, the color being the result of a combination of the colors of the two components. The fungus lives parasitically on the alga, from which it absorbs food, the alga manufacturing food for itself and for the fungus component of the lichen; the fungus in turn protects the alga from drying out in very dry situations. The fungus hyphae which absorb food from the algae are in very intimate contact with them (Fig. 774).

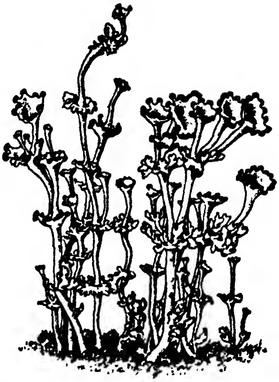


FIG. 771. *Cladonia verticillata.* (× ½)

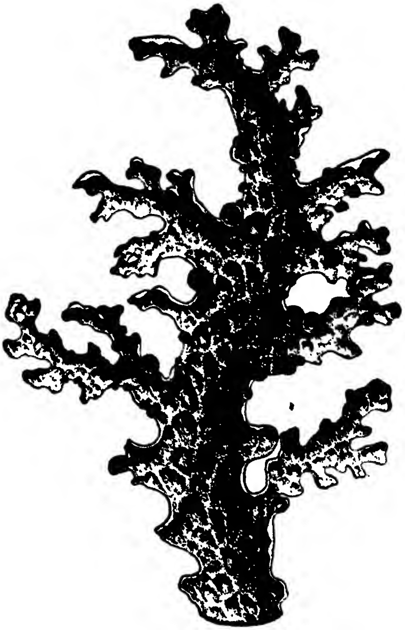


FIG. 772. ***Lobaria pulmonaria*****, a lichen with a thallus form and cup-shaped fruit bodies.** (× 1)

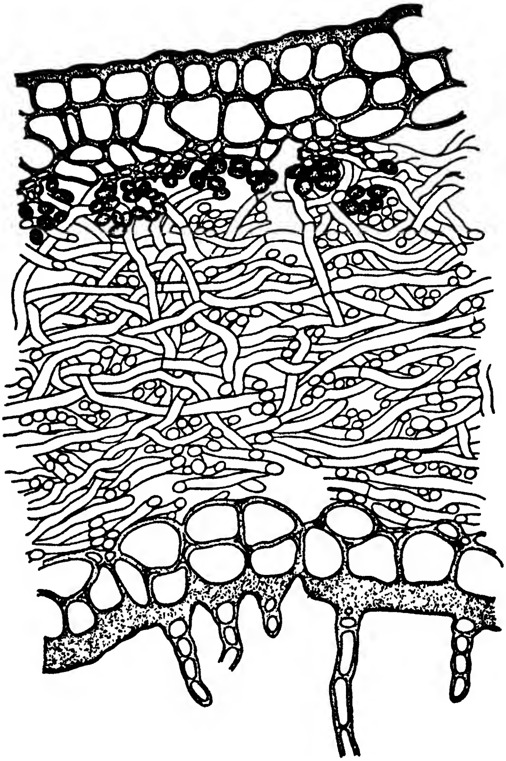


Fig. 773. Cross section of a lichen thallus

The dark oval bodies near the upper portion of the thallus are algal cells

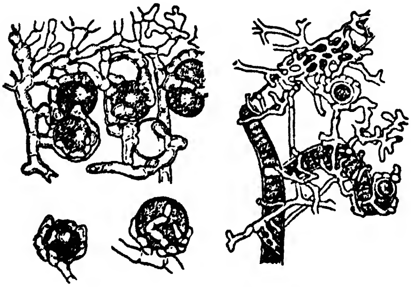


Fig. 774. Relation of fungi to algae in lichens

Left, *Cladonia furcata*, in which the lichen is a green alga belonging to the *Chlorococcales* (× 475). Right, *Stereocaulon ramulosum*, in which the alga is a *Scytonema*, one of the *Cyanophyceae* (× 325). After Bornet

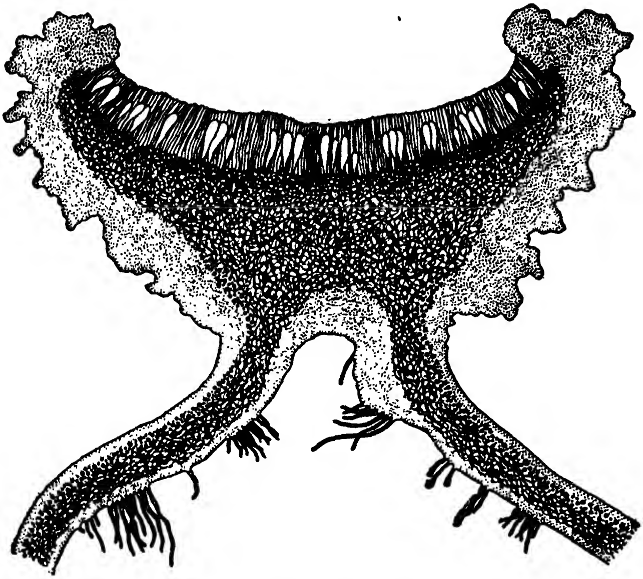


Fig. 775. Cross section through a whole lichen fruit body and portion of adjoining thallus

Note the algal cells showing as dark spots in the upper part of the thallus; note also the hymenium lining the cup. (× 40)

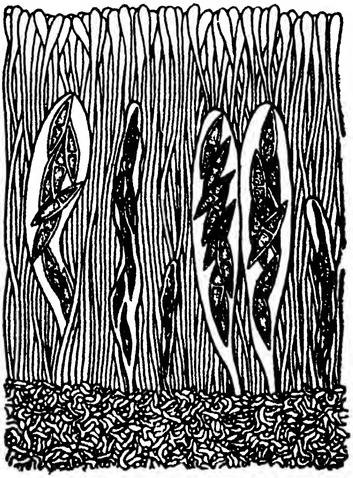


Fig. 776. Cross section of a portion of the hymenium of a lichen fruit body, showing asci and paraphyses. (× 320)

Lichens live in a great variety of habitats, as on exposed rocks, on the bark of trees, or on the ground. Some hang from the smaller branches of trees (*Usnea*, Fig. 770). The so-called reindeer moss is not a moss but a lichen (*Cladonia rangiferina*). The combination of fungus and alga is able to live in exposed places, for instance on bare rocks or exposed limbs of trees, where neither of the constituents could survive alone. Lichens can withstand long periods of drying. The upper and lower layers of lichens are usually dense and composed of thick-walled hyphae, while the interior has a looser and more spongy structure (Fig. 773).

Lichens are often reproduced by the formation of special reproductive structures known as *soredia*. These are small balls which are formed on the surface of the lichens; each consists of fungus hyphae enclosing a few algal cells. In one genus of lichens the fungus component is a basidiomycete, which reproduces by basidiospores. In most cases the fungus is an ascomycete and produces ascocarps in which are numerous asci containing ascospores (Figs. 775, 776).

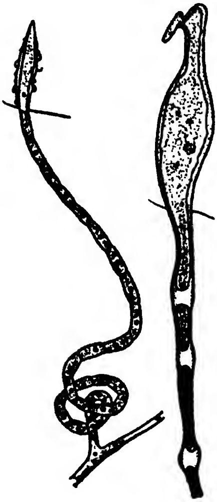


Fig. 777. Ascogonium and trichogyne of lichen, *Collema crispum*

Left, coiled ascogonium with long trichogyne (× 270); right, end of a trichogyne with spermatium attached (× 750). After Baur

In some of the ascomycetous lichens there are structures which have been interpreted as ascogonia, and also spermatia which are produced in much the same way as the spermatia of rusts. The ascogonia are multicellular and coiled, and terminate in long multicellular trichogynes which reach to the surface of the thallus. In one case the spermatium has been described as fusing with the trichogyne and its nucleus as passing into the trichogyne (Fig. 777). The middle cells of the ascogonium grow out to form asci. Migration of the male nucleus to the ascogonium has been surmised but not demonstrated. Some see in this type of fertilization a suggestion of descent from red algae. Those who regard the *Zygomycetes* as ancestors of the fungi take the view that the spermatia are to be regarded as conidia which have taken the place of antheridia. This question has been discussed in connection with the origin of the *Ascomycetes*.

CHAPTER XXVI

DIVISION *BRYOPHYTA*

General characteristics. The bryophytes are small plants. The division is composed of two classes, the *Hepaticae* (liverworts) and the *Musci* (true mosses). Whereas the algae are predominantly water plants and only a few simple ones have become secondarily adapted to aerial conditions, the *Bryophyta* are predominantly land plants with only a few that grow in water. They are the simplest types of green plants which are true land plants.

The conspicuous plants of the *Bryophyta* are gametophytes, which produce eggs and spermatozoids. In mosses the gametophyte is differentiated into a central axis or stem with small spirally arranged leaves (Figs. 806, 817). In some of the liverworts the gametophytes are thallus plants (Figs. 791, 798); in others they have stems and delicate leaves (Fig. 800). In those with stems and leaves there are two dorsal rows of leaves arranged along the sides of the stem, and usually a small third row on the ventral surface. The leaves of most mosses have a midrib, but such a structure is not found in any of the liverworts.

Bryophytes do not have roots, but are anchored to the substratum by hairlike rhizoids (Figs. 806, 817). The female reproductive organ of the bryophytes is an archegonium (Fig. 780). This is a flask-shaped structure which, when mature, contains a single egg. Spermatozoids are borne in large numbers in antheridia (Fig. 781). The development of the fertilized egg results in the production of a sporophyte, which in most cases consists of a sporangium, or capsule, a stalk, and an absorbing organ, or foot, which absorbs material from the parent plant (Fig. 795). In a few species of simple liverworts the sporophyte is a sporangium without stalk or foot (Figs. 782, 783). In all cases the gametophytes and sporophytes are entirely different in both appearance and structure.

CLASS *HEPATICAE*

Gametophyte. Most of the *Hepaticae* live on the land in moist places, while a few may grow in water. Some of them are found on the ground and others on the trunks, branches, or leaves of other plants. The gametophytes of the liverworts are always small or relatively small plants, but are always large enough to be readily visible. Although the thallus forms (Fig. 778), when examined closely, are very unlike mosses, all liverworts would probably be regarded as mosses by people not familiar with botany.

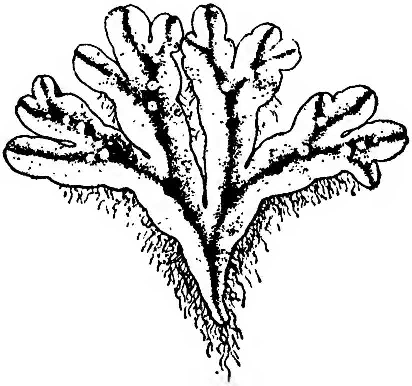


FIG. 778. Thallus of *Riccia*

The dark rounded bodies are mature sporophytes which are embedded in the thallus, while the lighter bodies are immature sporophytes. (× 2)

Sexual reproduction. The eggs are borne singly in oogonia, called archegonia (Figs. 779, 780). An archegonium of a liverwort is a flask-shaped structure, the wall of which is composed of a single layer of cells. The lower part of the archegonium is enlarged and contains a single large cell. This, shortly before the archegonium matures, divides into two cells, the lower of which is a large egg, while the upper is smaller and is known as the ventral canal cell (Fig. 779). The upper portion of the archegonium is elongated into a narrow structure called the neck, within which is a row of cells, the neck canal cells. When the archegonium matures, the ventral canal cell and neck canal cells become disorganized and the top of the neck opens to discharge the remains of the canal cells (Fig. 780), after which the spermatozoids can swim through the neck to the egg cell.

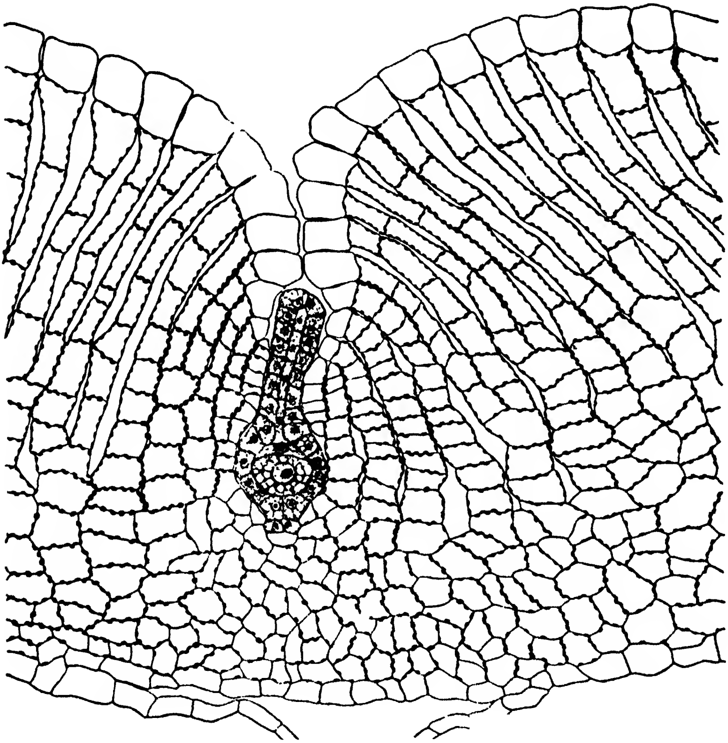


FIG. 779. Section of a portion of the thallus of *Riccia*

In the center is an immature archegonium; the enlarged venter contains a large egg and above this a ventral canal cell; in the neck there are four neck canal cells. Most of the cells of the thallus show chloroplasts. Note the vertical rows of cells which project upward from the upper surface of the thallus. The terminal cell of each row is enlarged and lacks chloroplasts. These terminal cells are close enough together to form a layer which serves as an epidermis. (× 190)

The antheridium of a liverwort is usually somewhat oval (Fig. 781), and consists of an inner portion, composed of numerous fertile cells, surrounded by a single layer of sterile cells. The fertile cells give rise to biflagellate spermatozoids (Fig. 781).

Fertilization takes place by the swimming of a spermatozoid to the egg in the archegonium, and the fusion of the spermatozoid with the egg. ✓Owing to the fact that the spermatozoids have no other means of reaching the archegonia than by swimming through water, it is evident that water is necessary for the accomplishment of fertilization. This indicates that the *Hepaticae* are descended from an algal ancestor which lived in water, and in which fertilization was also accomplished by means of motile spermatozoids.✓

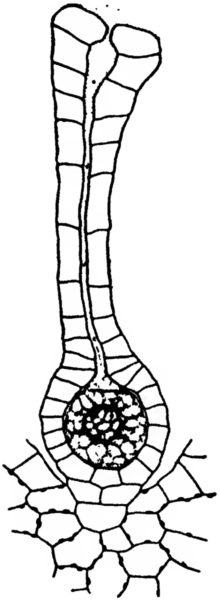


Fig. 780. Mature archegonium of *Riccia*

The neck canal cells and ventral canal cell have become disorganized. (× 240)

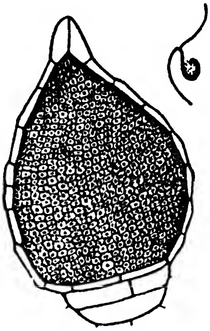


Fig. 781. Antheridium (× 160) and a single spermatozoid of *Riccia*

The antheridium consists of a stalk, a covering of sterile cells, and many sperm cells

Sporophyte. The fertilized egg of the *Hepaticae* germinates immediately within the archegonium; but instead of giving rise to a thallus it produces a structure in which spores are formed (Figs. 782, 783). This structure is therefore a sporophyte. The spores, on germination, produce a gametophyte. The sporophyte in its simplest form consists of a single sporangium (Figs. 782, 783), but in most of the *Hepaticae* it is a sporangium with a stalk and an absorbing organ, the foot, which attaches the sporophyte to the gametophyte (Fig. 795). In all cases a nearly mature sporangium contains a considerable number of rounded cells which are known as spore mother cells. Each of these divides to form four spores. At least in their early stages, the four spores derived from a mother cell hold together in a group and are flattened on the sides where they come in contact. A group of four spores derived from a spore mother cell is known as a tetrad.

Alternation of generations. The gametophyte that produces eggs and spermatozoids is followed by a sporophyte that produces spores, and this in turn by a gametophyte. There is therefore an alternation between a gametophyte, which produces eggs and spermatozoids, and a sporophyte, which gives rise to spores. This alternation of gametophytes and sporophytes is an alternation of generations, or an alternation of a gametophytic and a sporophytic generation (Fig. 784).

Some of the green algae show an alternation of generations; so do most of the brown and of the red algae. This alternation of generations is found not only in all the *Bryophyta* but in all higher plants. It is generally believed that the green land plants are descended from the green algae, and it may be that the alternation of generations which is so universal in the higher plants originated in some algal ancestor. In the development in the plant kingdom, however, it appears that an alternation of generations has originated independently in various lines. It is doubtful if any alter-

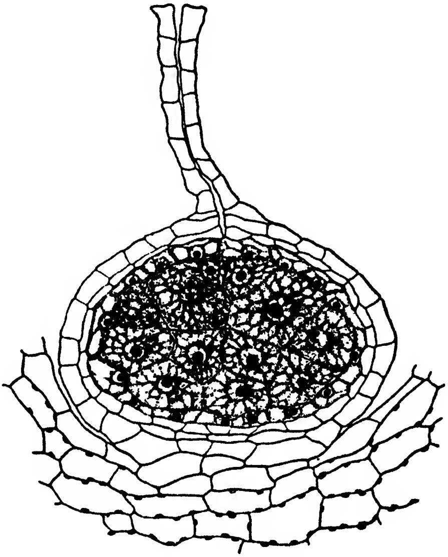


Fig. 782. Immature sporophyte of *Riccia* within the archegonium

The cells of the basal portion, or venter, of the archegonium have divided, so that this part of the archegonium consists of two layers of cells. At this stage the sporophyte consists of a considerable number of spore mother cells surrounded by a single layer of sterile cells. The nuclei and protoplasm are shown in the sporophyte and not in the tissue of the gametophyte. (× 140) nation of generations which we know in any of the algae has any relationship to that of the *Bryophyta* and other land plants.

Chromosomes and alternation of generations. As a result of the fusion of the nuclei of the egg and the spermatozoid, the fertilized egg has twice as many chromosomes as either the egg or the spermatozoid. In other words, the egg or the spermatozoid is haploid, while the fertilized egg is diploid. The diploid, or double, number of chromosomes persists in the sporophyte until spore mother cells are formed. Each spore mother cell, by two successive divisions, gives rise to four spores, and in these two divisions the number of chromosomes is reduced. Thus each spore has a single number of chromosomes; that is, it is haploid. These give rise to gametophytes which are haploid, and the double number is again restored when the egg is fertilized by a spermatozoid. The gametophyte is thus characterized by a haploid number of chromosomes and the sporophyte by a diploid number. The alternation of generations is therefore not only an alternation of a gametophytic and a sporophytic generation, but also an alternation of a haploid and a diploid generation. As the spore mother cell is diploid and the spores hap-

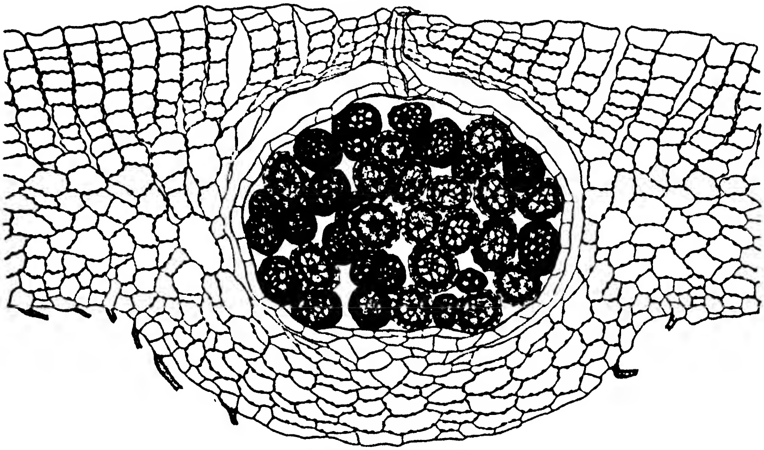


Fig. 783. Section of thallus of *Riccia*, showing mature sporophyte

The sporophyte, or sporangium, at this stage consists of a mass of spores, the sterile covering having disappeared. The spores lie free in the venter of the archegonium, the inner layer of cells of which has practically disappeared. (×80) loid, the sporophytic generation ends with the spore mother cell; the spore is the beginning of the gametophyte. This alternation of a haploid gametophyte and a diploid sporophyte is characteristic of the bryophytes, pteridophytes (ferns and their allies), and spermatophytes (seed plants).

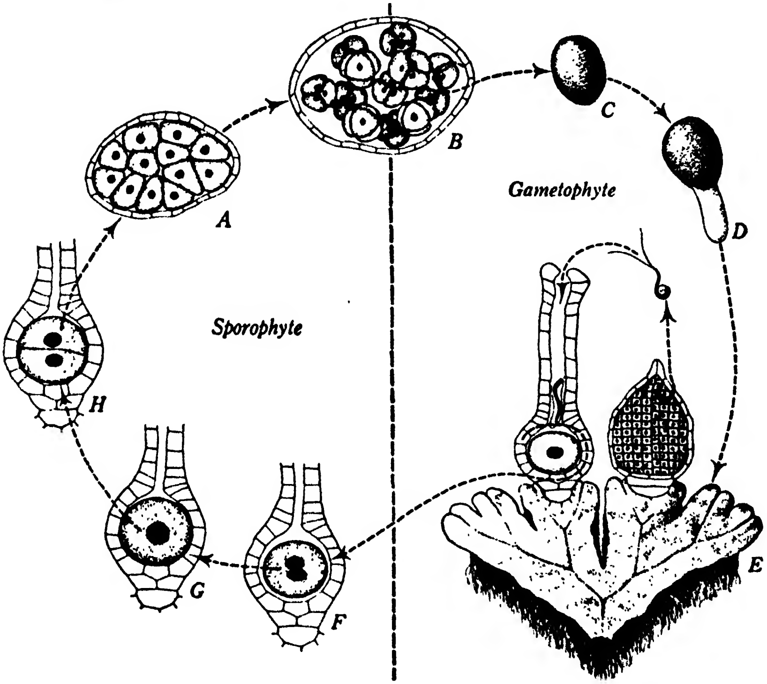


FIG. 784. Diagram of life cycle in *Riccia*

A, sporangium with spore mother cells; this is the complete sporophyte. *B*, sporangium with tetrads of spores; the line separating the sporophyte and the gametophyte is drawn through the sporangium because the sporangium belongs to the sporophyte while the gametophyte begins with the spore. *C*, a single spore. *D*, spore germinating. *E*, prothallus formed from spore; a spermatozoid is represented as leaving an antheridium and entering an archegonium. *F*, an egg, with egg and spermatozoid nuclei in contact; the sporophyte begins with the fertilized egg. *G*, the two nuclei have fused to form the primary nucleus of the sporophyte. *H*, this primary nucleus has divided

Orders of the *Hepaticae*. The *Hepaticae*, or liverworts, contain four orders: the *Ricciales*, the *Marchantiales*, the *Jungermanniales*, and the *Anthocerotales*.

Order *Ricciales*

Gametophyte of *Riccia*. The genus *Riccia* may be taken as an example of the *Ricciales.* The gametophyte is a dichotomously branching thallus (Fig. 778). The term "dichotomous branching" denotes a system of branching in which the main axis forks repeatedly into two equally developed parts.

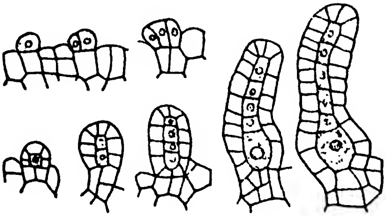


Fig. 785. Development of archegonia of *Riccia natans*

Note that a single cell projects from the surface; that the first divisions of this cell are longitudinal and separate a central cell from surrounding cells which will form the wall of the archegonium; later, a cross division cuts off a cell which by dividing will form the sterile covering cells at the top of the archegonium. The center cell divides transversely to form the egg, ventral canal cell, and neck canal cells. (After Lewis)

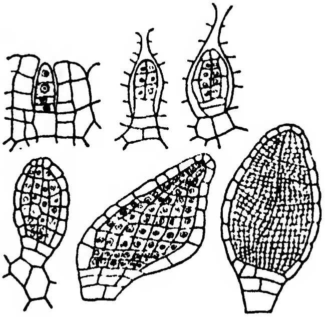


Fig. 786. Stages in development of antheridium of *Riccia natans*

After Lewis

The gametophyte of *Riccia* grows in length by means of an apical cell. The thallus has very numerous rhizoids. These act like root hairs and serve both to attach the thallus to the substratum and for the absorption of water and minerals. From the upper surface of the main body of the thallus there project upwards vertical rows of cells which are separated from each other by fairly wide spaces (Fig. 779). The upper cell of each row is larger than the cells below it. These upper cells fit together to form a sort of epidermis.

Antheridia and archegonia. The archegonia (Figs. 779, 780, 785) and the antheridia (Fig. 786) are borne singly in a groove which extends longitudinally through the center of the upper part of the thallus (Fig. 786). In *Riccia* both antheridia and archegonia are found on the same plant, so that *Riccia* is a monoecious type.

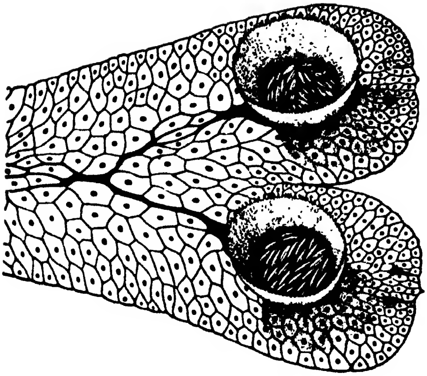


Fig. 787. Portion of a thallus of *Marchantia* bearing two gemma cups within which are many gemmae

The lines dividing the thallus into polygonal areas mark the boundaries of air chambers, while the black dots represent the stomalike openings into the chambers. (× 6)

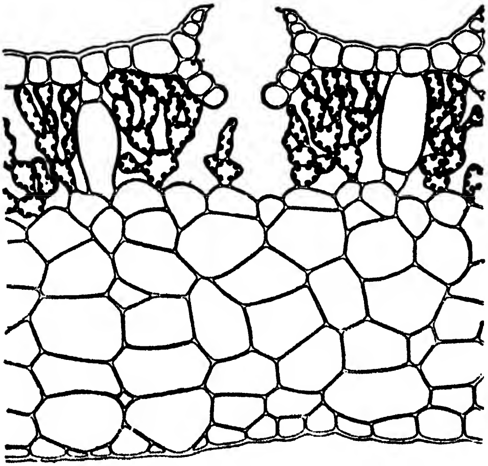


Fig. 788. Section of a portion of a thallus of *Marchantia*

Below, colorless tissue; above, air chambers with phototosynthetic cells. Note the stomalike opening into the central chamber and the large cells which form the side walls of the chambers. (× 200)

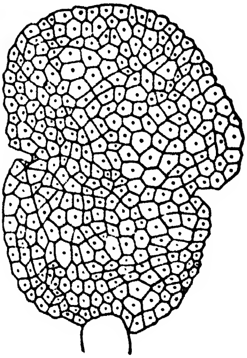


Fig. 789. Gemma of *Marchantia* after the rupture of the stalk cell. (× 150)

Note the stalk cell below, and on either side the notches where growth will begin

The antheridia and the archegonia are formed near the tip; the youngest of them are found nearest the tip, and the older ones progressively farther from the tip.

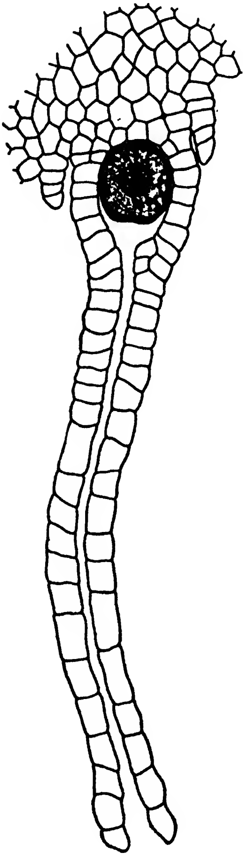


Fig. 790. Archegonium of *Marchantia*. (× 175)

Sporophyte. The fertilized egg develops inside of the archegonium. It gives rise to a single rounded sporangium without a stalk (Fig. 782). This sporangium consists of an outer layer of sterile cells and numerous cells which produce spores (Fig. 782).

The sporangium wall is an evanescent structure which almost entirely disappears before the spores are mature. As a sporangium grows, the base of the archegonium enlarges and comes to be composed of two layers of cells (Fig. 782). The inner of these layers, like the wall of the sporangium, disintegrates (Fig. 783). After the disintegration of the sporangium wall the mature spores lie free in the cavity of the enlarged archegonium, and are surrounded by the outer layer of cells of the archegonium wall (Fig. 783). The mature sporangium is therefore nothing more than a mass of spores.

The sporophyte of *Riccia* lacks chlorophyll and is entirely dependent on the gametophyte for nourishment. The sporophyte of the *Ricciales* is the simplest one found in the bryophytes. When a spore germinates, it produces a thallus bearing archegonia and antheridia (Fig. 784).

Order *Marchantiales*

Marchantia. The *Marchantiales* represent a higher development of the *Ricciales*. *Marchantia* is one of the most highly developed of the *Marchantiales*. It appears to be quite different from *Riccia*, therefore, but there is such a complete series of forms leading from the typical *Ricciales* to *Marchantia* that some botanists prefer to include the *Ricciales* in the *Marchantiales*. *Marchantia* is dioecious, as the antheridia and archegonia are borne on separate plants on special upright umbrellalike branches.

The main part of the gametophyte is a flat dichotomously branched thallus (Figs. 787, 791), in which respect it resembles *Riccia*. It grows in length by an apical cell.

From the lower surface there arise numerous rhizoids which serve as anchoring and absorbing organs. The thallus is several cells in thickness. The upper portion is divided into polygonal air chambers, each of which has a central chimneylike opening (Fig. 788). Within each chamber is a loose arrangement of assimilative cells with chloroplasts. The outlines of the chambers are plainly visible from the exterior and give the thallus a very characteristic appearance (Fig. 787).

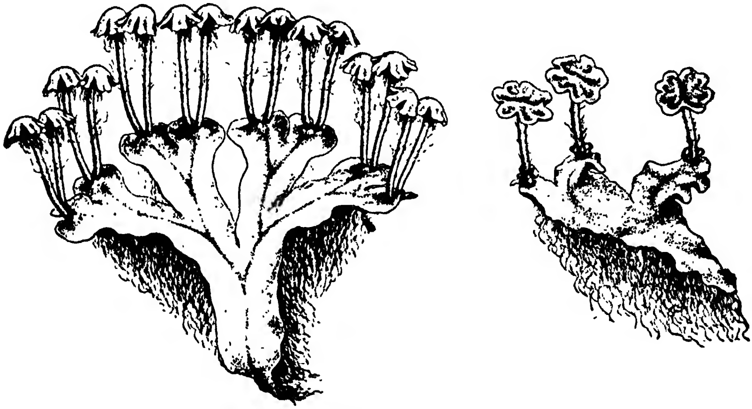


FIG. 791. *Marchantia*

Left, female plant with specialized branches which bear archegonia on their under surfaces; right, male plant with specialized branches which bear antheridia sunken in the upper surface. (× 1½)

Gemmae. The gametophyte of *Marchantia* has a very specialized method of asexual reproduction. This is by means of gemmae which are produced within cuplike structures called gemma cups (Fig. 787). A gemma originates as a unicellular outgrowth from the base of the cup. The upper portion of the gemma becomes enlarged and lens-shaped with a notch at either side (Fig. 789). After the gemmae are detached and scattered, they germinate if suitable

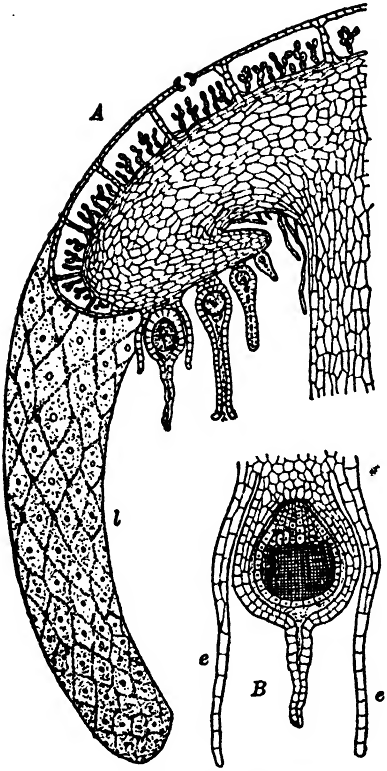


Fig. 792. An archegonial branch of *Marchantia*

A, portion of a lengthwise section of a young archegonial branch (semi-diagrammatic), showing a row of archegonia hanging down from the lower surface, the youngest being nearest the stalk: air chambers are present on the upper surface; *l*, one of the finger-like lobes back of the section, the diamond-shaped areas indicating air chambers. *B*, a young sporophyte within the parent archegonium: the region which is to become the spore case is indicated by the cross lines, and the small foot is attached to the base of the archegonium; *e*, a special envelope developed around the archegonia of *Marchantia*

conditions are present. A growing point is located in each notch, and so growth from a gemma starts in two opposite directions.

Archegonia and antheridia. The archegonia (Fig. 790) are found on the lower surfaces of special branches which grow on female plants (Figs. 791, 792), while the antheridia (Fig. 793) are sunk in the upper part of somewhat similar branches on male plants (Fig. 791). The antheridia and archegonia are very similar to those of the *Ricciales*. The umbrella shape of the reproductive branches is due to the repeated forking of the apical cells. This results in the radial arrangement of the umbrellalike top, and in the arrangement in rows of both archegonia and antheridia. The stalk of an archegonial branch when ready for fertilization is very short, and so (Fig. 797) spermatozoids swimming in water on the surface of the vegetative portion of the thallus can reach the archegonia. After the eggs are fertilized, the stalk elongates and carries the developing sporophytes up into the air (Fig. 791).

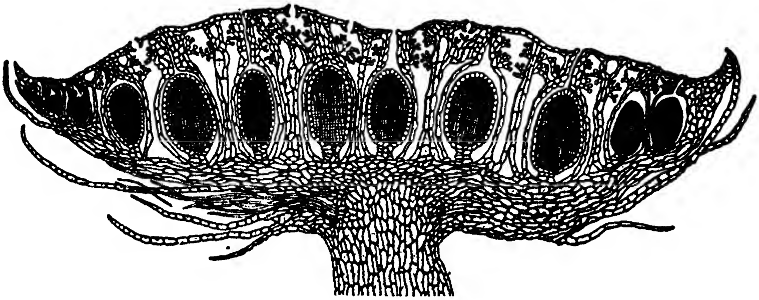


Fig. 793. Section through an antheridial branch of *Marchantia*

Showing air chambers, and also ovoid antheridia containing many sperm cells. (× 30)

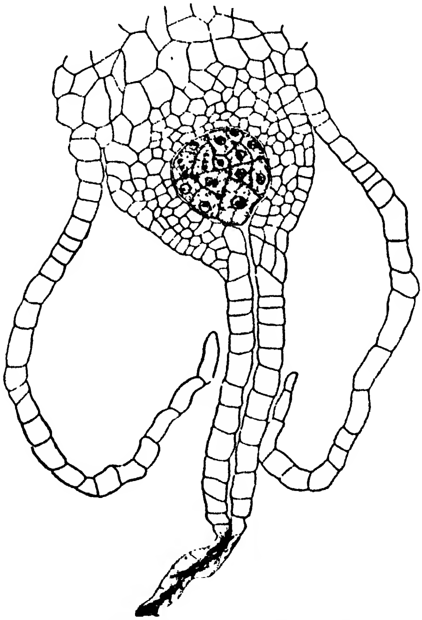


Fig. 794. Young sporophyte of *Marchantia* enclosed within an archegonium

The tip of the archegonium is disorganizing. (× 135)

The fertilized egg germinates within the archegonium and develops into a sporophyte (Fig. 794). This is more complicated than that of *Riccia* in that it consists of three parts: a rounded sporangium, an elongated stalk, and an absorbing structure, the foot, which is imbedded in the tissue of the umbrellalike top of the archegonial branch (Fig. 795). The sporophyte of *Marchantia,* like that of *Riccia,* is without chlorophyll and is entirely dependent on the gametophyte for nourishment. This is absorbed through the foot. As the sporophyte develops, the archegonium enlarges and remains as a cover around it. This covering is known as the calyptra. As

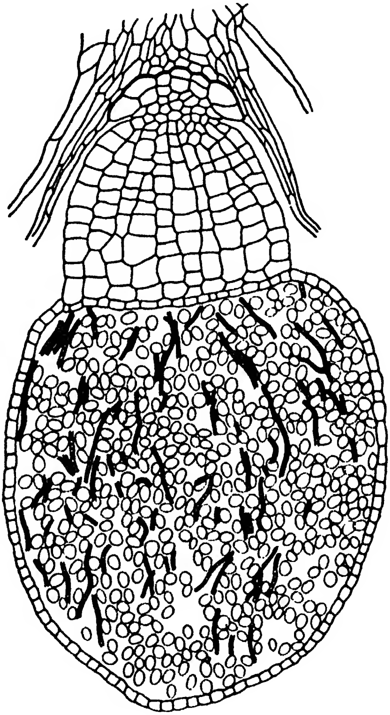


Fig. 795. Sporophyte of *Marchantia* before elongation of the stalk

Below is the large sporangium; above this is the stalk, and above the stalk the foot embedded in the archegonium. The upper limit of the foot is shown as a dark line. Note portions of elaters among the spores. (× 85) the sporangium is maturing, the stalk elongates rapidly and shoves the sporangium through the calyptra. This elongation of the stalk carries the sporangia downward so that they are freely exposed to the wind (Fig. 796). The spores are thus in a favorable position for dissemination by wind when the sporangial wall ruptures. The sporophyte of *Marchantia* is more complicated than that of *Riccia* not only in that it has a foot and a stalk in addition to a sporangium, but also because some of the cells in the sporangium remain sterile and form elaters. These are greatly elongated cells with spiral thickenings (Fig. 797). They are hygroscopic and bend and twist with changes in humidity, and in this way assist in scattering the spores.

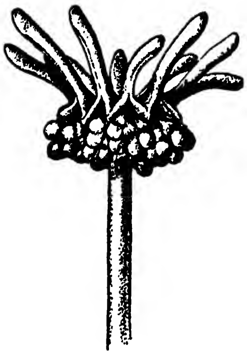


Fig. 796. Vertical branch of female thallus of *Marchantia* with many sporophytes. (× 2½)

The complicated mechanism for the dissemination of the spores of *Marchantia* is in marked contrast to the lack of any special method in *Riccia*. In the latter the spores are set free only after the disintegration of the thallus. In *Marchantia* the elongation of the stalk of the archegonial branch carries the sporangium up into the air, while the elongation of the stalk of the sporophyte places it in a freely exposed position; elaters then take part in the scattering of the spores.

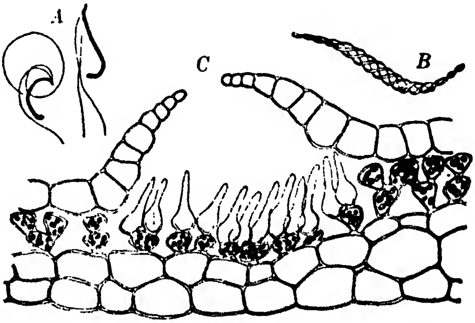


Fig. 797. ***Conocephalus conicus*, one of the *Marchantiales* closely related to *Marchantia***

A, two spermatozoids; *B*, an elater; *C*, section of air cavity. (*A*, *B*, after Bolleter)

A spore of *Marchantia* germinates directly and forms a gametophytic thallus which, as we saw, bears archegonia and antheridia.

Relationship. The *Marchantiales* seem to be clearly derived from some such plants as the *Ricciales* and to represent a line of evolution in which the gametophytes have developed into complicated and interesting structures. As far as is known, the *Marchantiales* have never given rise to anything higher than themselves.

Order *Jungermanniales*

Some of the members of this order have a simple thallus (Fig. 798), but in most cases the thallus is differentiated into stems and leaves (Fig. 800). The stems do not show a differentiation of tissues and have no specialized conducting cells. A leaf consists of a single layer of cells without a midrib. The archegonia and the antheridia are similar to those of the two previous orders. The fertilized eggs develop into a sporophyte (Fig. 801) similar to that of the *Marchantiales* in that it consists of a sporangium, a foot, and a stalk.

The sporophyte of the *Jungermanniales* is more complex than that of the *Ricciales*, but the simplest thalli found among the *Hepaticae* occurs in some of the thallus members of this order.

Order *Anthocerotales*

Anthoceros. The gametophyte of the *Anthocerotales* is a simple thallus, but the sporophyte is more complicated than that of any other order. *Anthoceros* (Fig. 802) may be taken as an example. In this genus the sporophyte (Fig. 803) consists of a basal absorbing organ, the foot, and a terminal club-shaped sporangium. Near the base there is a meristematic region, the activity of which causes the sporangium to increase in length. The outer part of the sporangium consists of sterile cells, and in the center there is a column of sterile cells, the columella. The spores are formed between these two sterile regions. As the spores in the tip of the sporangium reach maturity the upper part of the sporangium splits and the spores are liberated (Fig. 802). As more spores mature the sporangium continues to split. In this way the sporangium is continually liberating spores, while new spores are being produced as the result of the activity of the basal meristem.

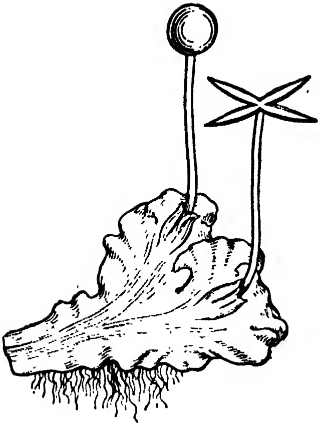


Fig. 798. Thallus of *Pellia* (one of the *Jungermanniales*) with unopened and opened sporophyte. (× 2)

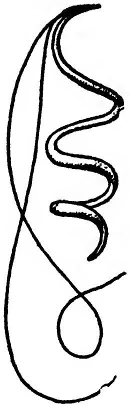


Fig. 799. Spermatozoid of *Pellia epiphylla.* (× 1400)

After Guignard

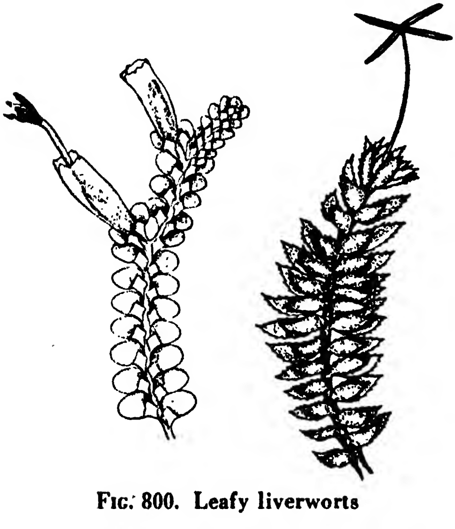


Fig. 800. Leafy liverworts

In the drawing at the left each leaf consists of a large and a small lobe; on the left side there is a sporophyte which has elongated out of the perianth and has opened; above this sporophyte is another which is still enclosed within the perianth (× 4). In the drawing at the right, each leaf consists of a large and a small lobe (× 1)

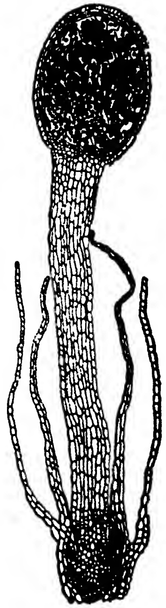


Fig. 801. Longitudinal section through sporophyte of *Ptilidium*, one of the *Jungermanniales*

The sporophyte consists of a sporangium, stalk. and foot. (× 20)

While the thalli of the *Anthocerotales* are simple, the sporophytes are the most advanced found in the *Hepaticae.* They resemble the sporophytes of the *Musci,* and also those of the *Pteridophyta* and *Spermatophyta,* in having stomata and assimilating tissue with chlorophyll. Owing to the presence of chlorophyll the sporophyte is only partially dependent on the gametophyte. If the foot of the sporophyte of *Anthoceros* were developed into a root, the sporophyte would be an independent plant.

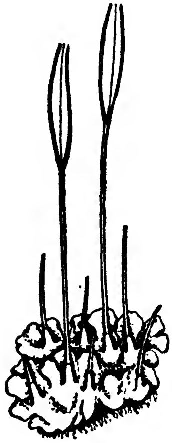


FIG. 802. Thallus of *Anthoceros* with six young unopened sporophytes and two long sporophytes which have split and show the columellae in the center. (× 1½)

Relationship of *Hepaticae.* Most botanists have long believed that the liverworts represent an early stage in the development of land plants and that they gave rise to the ferns, lycopods, and all higher plants. The gametophyte of a liverwort, according to this theory, is hardly more than an algal thallus which has left the water and come to live on the land. In support of this view it may be pointed out that the gametophyte has a very simple structure without a vascular system or roots and, in what are regarded as the more primitive types, not differentiated into stems and leaves. Also, many forms can live only in very damp places, and all have swimming spermatozoids, which necessitate the presence of actual water for the process of fertilization. The sporophyte of the *Hepaticae* is regarded as essentially a new structure, characteristic of land plants, and it is the development of the sporophyte that has led to the evolution of the higher plants. According to this theory the liverworts developed from a simpler form than any known at present. This form must have combined a sporophyte at least as simple as that of *Riccia* with a gametophyte which was no more complicated than that of the simplest of the thallus *Jungermanniales.* From such a simple ancestral form we can think of development as

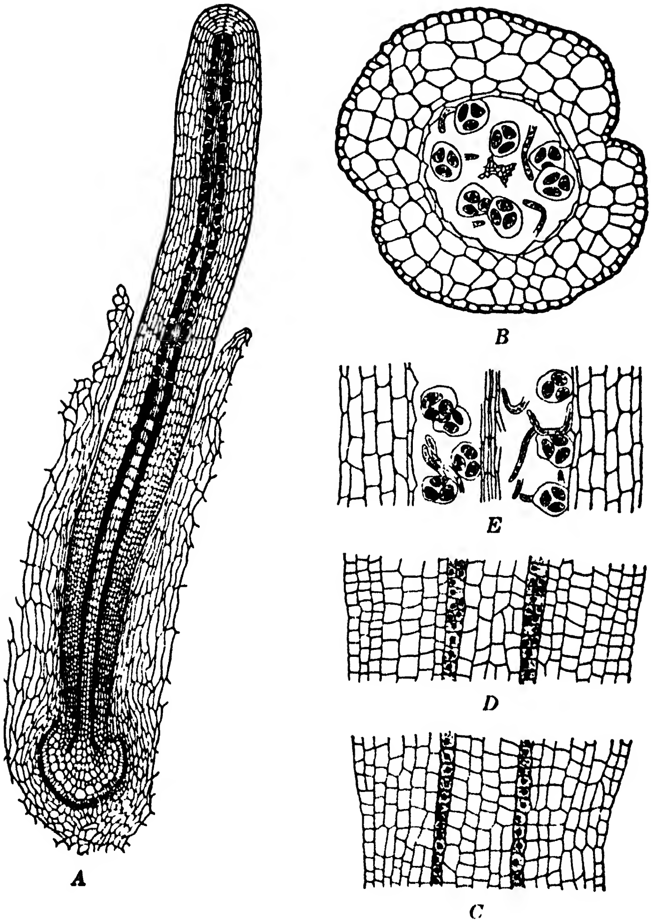


FIG. 803. *Anthoceros*

A, section through sporangium and surrounding portion of thallus (× 31). The lower part of the sporophyte is a foot, above this is a meristematic region, and still higher up are progressively older stages in the formation of spores. Note the sterile columella in the center and the sterile tissue surrounding the spore-bearing portion. In the drawing the sporogenous tissue is darker than the sterile tissue. *B*, cross section of sporangium showing columella in the center surrounded by sporogenous region. *C*, *D*, *E*, show successive stages in spore formation as seen in longitudinal section (× 105) having taken place in three directions. The first line leads through the *Ricciales* to the *Marchantiales* and culminates in such complicated forms as *Marchantia.* The second line proceeds from the simple thallus *Jungermanniales* to the more complicated types of the leafy *Jungermanniales.* In the third line we see the development from the simpler *Anthocerotales* to *Anthoceros.*

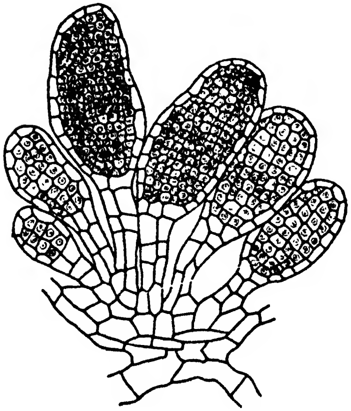


Fig. 804. A group of antheridia of *Anthoceros*

Each antheridium consists of a stalk, a covering of sterile cells, and many sperm cells. (× 215)

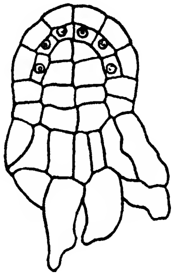


Fig. 805. Longitudinal section of young embryo of *Anthoceros pearsoni*

The cells with nuclei will give rise to spore-producing tissue. (After Campbell)

Many features found in the liverworts indicate an ancestry among the green algae. These include the same type of pigmentation as in the green algae; the storage of food in the form of starch; and biflagellate spermatozoids.

CLASS *MUSCI* (MOSSES)

General characteristics. Mosses are fairly small plants in which the gametophyte, during the greater part of its life, consists of a stem with small leaves (Fig. 806). The sporophyte is conspicuous to the naked eye, and appears as a large characteristic capsule at the end of a long stalk (Fig. 806). In nearly all cases there is a distinct midrib in the leaf. The presence or absence of a midrib is often a convenient way of distinguishing between leafy liverworts and mosses. Usually the mosses can also be distinguished from the leafy liverworts by the fact that their leaves are

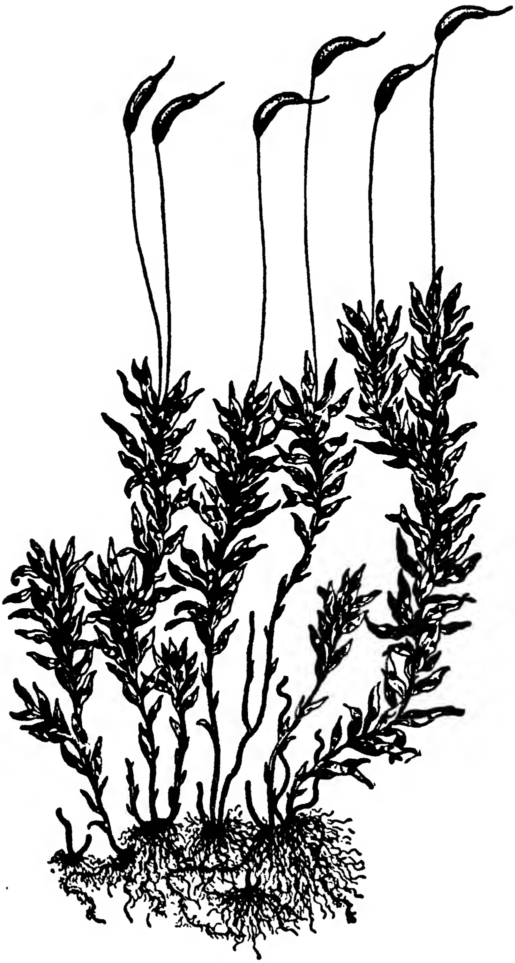


FIG. 806. A common moss (*Catharinea undulata*)

Showing the branching leafy moss plants (gametophytes) attached to the root-like mass of protonemal filaments and bearing sporophytes. (After Sachs)

spirally arranged. Nearly all mosses have not only a midrib containing conducting cells, but also a central strand of conducting tissue in the stem. Mosses do not have roots, but are abundantly supplied with rhizoids.

The gametophytes produce archegonia and antheridia which, while different in details, bear a general resemblance to those of the liverworts. The spermatozoids, like those of the liverworts, are biflagellate. The fertilized egg germinates within the archegonium and develops into a sporophyte which is permanently attached to the gametophyte by a foot as in the liverworts. The sporangium, or capsule, of the mosses is a very specialized structure (Fig. 818). Mosses are much more numerous than liverworts both in species and individuals, but they are much more uniform in structure.

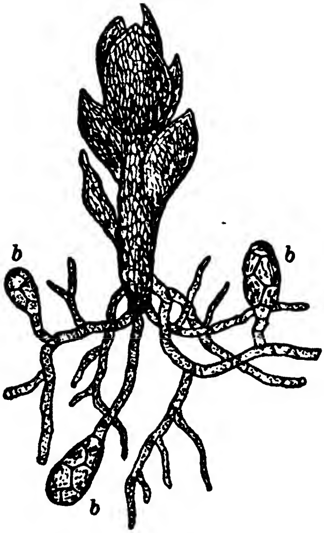


Fig. 807. A young plant of a common moss (*Webera*)

Showing its attachment to the protonemal filaments which bear reproductive buds *b*

Most mosses grow on the ground, and mosses may cover considerable areas. They often grow on tree trunks; in the cloud belt on tropical mountains they may form thick coatings on the trunks and branches of trees. Mosses also occur in various other situations, as on decaying wood and either damp or exposed rocks.

The first stage of a moss gametophyte is known as the protonema (Fig. 807). The cells of the protonema contain chlorophyll, and the protonema is an independent plant manufacturing its own food. In most mosses this is a branched, filamentous, algalike structure from which the leafy shoots arise as buds. In a few of the most primitive mosses the protonema is a thallus resembling a small, simple thallus gametophyte of a liverwort.

Order *Sphagnales*

***Sphagnum*.** All of the *Sphagnales* belong to the genus *Sphagnum*, which is generally regarded as the most primitive of the

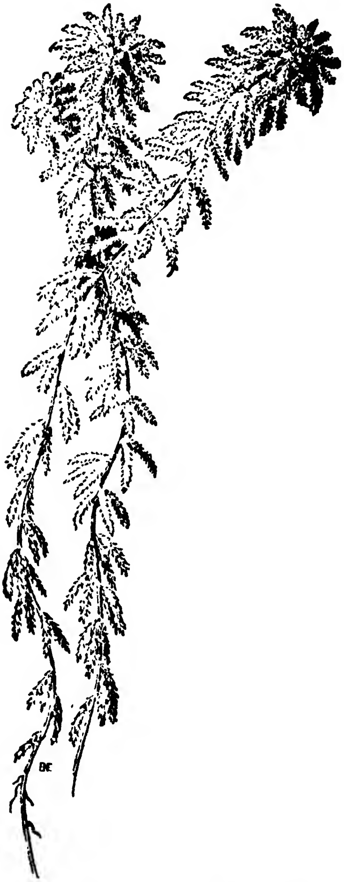


FIG. 808. The peat moss (*Sphagnum*)

mosses (Fig. 808). The protonema is a flat thallus from which a much-branched leafy shoot develops. The sporophyte is very different from that of the typical moss and much less complicated. It consists of a globular capsule and a foot, which are connected by a narrow neck (Fig. 809). During the development of the sporophyte it is, like that of *Marchantia*, surrounded by the enlarged archegonium, which forms a covering, or calyptra (Fig. 809). A large part of the capsule is occupied by sterile tissue. The spore cavity is dome-shaped and surrounds and overarches a sterile columella. At the top of the capsule is a cap, or operculum, which is separated from the remainder of the capsule by a groove. When the capsule is mature, the operculum comes off as a lid.

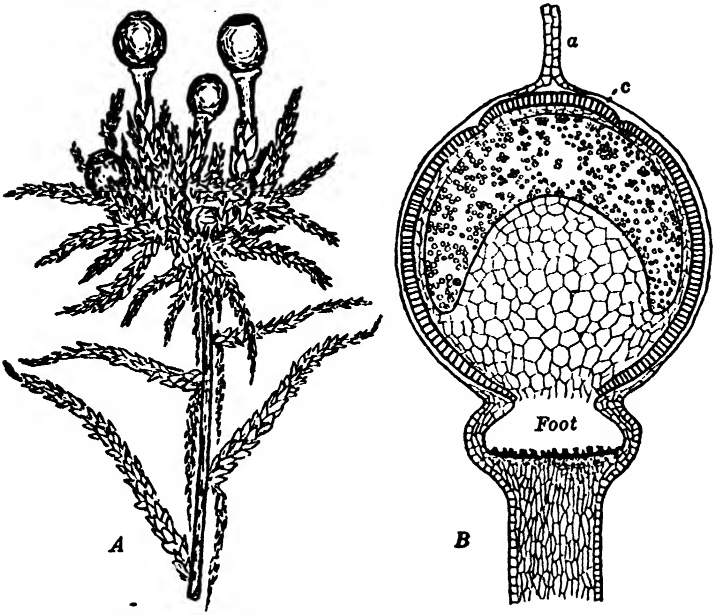


Fig. 809. The sporophyte of the peat moss (*Sphagnum*)

A, group of the sporophytes on stalks, which are really growths from the gametophyte. *B*, longitudinal section through a sporophyte, showing the large foot embedded in the top of the stalk: *a*, the remains of the parent archegonium, with the neck still present; *s*, spore chamber; *c*, cover, or operculum

Leaf of *Sphagnum*. The leaf of *Sphagnum* consists of a single layer of cells without a midrib. It is very peculiar in that it contains both living and dead cells. The living cells are small and form a network in the meshes of which are found the large dead cells (Fig. 811). The dead cells are transparent, and there is usually a circular opening in the wall. The dead cells are often filled with water, and it is due to their water-holding capacity that *Sphagnum* is useful for packing living plants. When dry, the leaves absorb liquids readily, and for this reason *Sphagnum* is useful for surgical dressings.

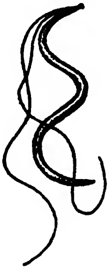


Fig. 810. Spermatozoid of *Sphagnum fimbriatum*

After Guignard

Relationship of *Sphagnum*. While there are many points of difference, the mosses are closely related to the liverworts and appear to have been derived from them. There are striking resemblances between *Sphagnum* and the *Anthocerotales*. Among these is the simple thallus protonema of *Sphagnum*. A very important point is the presence of stomata and chlorophyll in the sporophyte in both cases. Still another important point is that the spore-producing tissue of *Sphagnum* surrounds and overarches a sterile columella just as in young sporophytes of the *Anthocerotales*. In fairly young stages, before the capsule has expanded, the sporophyte of *Sphagnum* is strikingly like a young sporophyte of *Anthoceros* (Fig. 805).

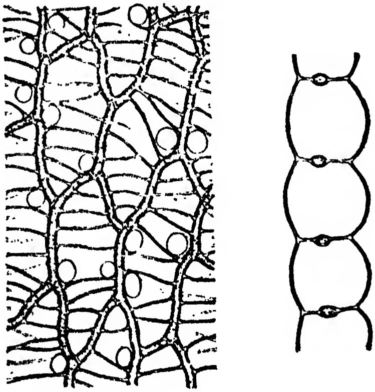


Fig. 811. Leaf of *Sphagnum*

Left, surface view; the thin shaded cells are the living cells with chlorophyll, the large areas enclosed by the living cells are the dead cells; note the conspicuous thickenings on the walls of these and the openings into them. Right, section of leaf cut across the view shown on the left; note the small living cells between the large dead empty cells

Peat mosses. Mosses are a prominent constituent of peat bogs. These occur in depressions containing fairly still water. The mosses grow in from the sides and form a floating mass. As the mosses and other plants associated with them continue to grow upward the lower layers are forced downward, and dead plant remains, known as peat, accumulate under the living cover. In the course of time the depression is filled, but the mosses, owing to their ability to absorb and hold large quantities of water, may continue to grow until the bog is raised considerably above its original level and even above the level of the surrounding area. The lower layers of plant remains become compressed and partially carbonized, forming peat. These deposits of peat are cut into blocks and used as fuel. Sometimes the peat is treated so as to improve its value as a fuel. *Sphagnum* is the chief peat moss.

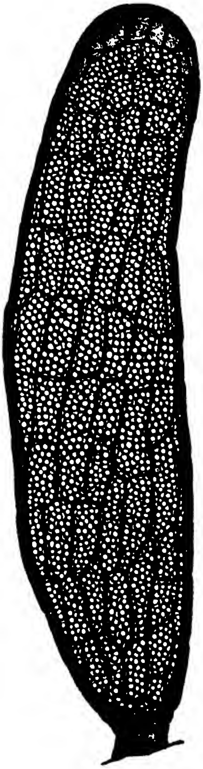


Fig. 812. A single antheridium of a moss. (× 155)

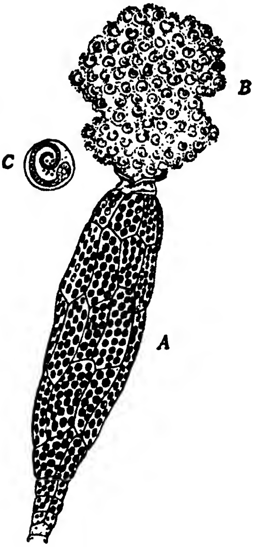


Fig. 813. The antheridium of a common moss (*Funaria*)

A, antheridium; *B*, escaping spermatozoids; *C*, a single spermatozoid, in its parent cell. (After Sachs)

Coal was formed by a process somewhat similar to that which gives rise to peat. The plants were different, and their remains accumulated not in bogs but as muck in the swamps or open waters of past ages.

Order *Bryales*

General characteristics. All of the mosses, except *Sphagnum* and a very small order which will not be considered here, are included in the *Bryales*. For so large a group, the structure is very uniform. The gametophyte is characterized by starting out as a filamentous protonema from which the leafy branches arise as buds (Fig. 807). It is characteristic of the *Bryales* to have the antheridia (Figs. 812, 813) or archegonia (Fig. 814) in groups at the ends of branches (Figs. 815, 816). The leaves around them are often slightly modified so that the fertile tip has something of the appearance of a flower. This is particularly true of the antheridial heads of some genera.

The capsule is borne at the tip of a long stalk, and is a rather highly developed and complicated affair (Figs. 817, 818). During the early stages of its life it is, like that of *Sphagnum* and *Marchantia*, surrounded by a calyptra formed from the archegonium. As the stalk expands, the calyptra is carried upward as a covering over the capsule (Fig. 817). Only a minor proportion of the tissue of the capsule

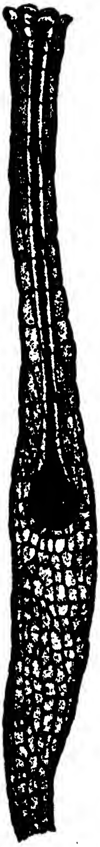


Fig. 814. A single archegonium of a moss. (× 150)

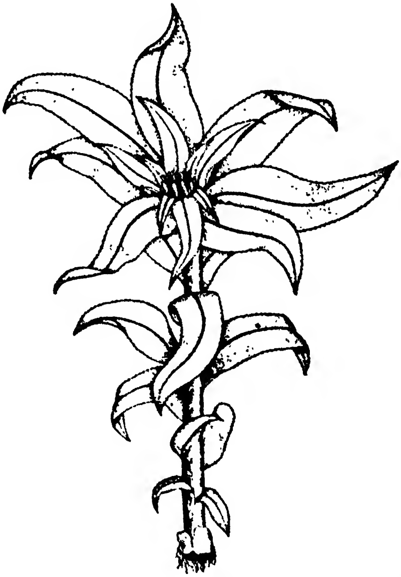


Fig. 815. Gametophyte of a moss, showing a group of antheridia and archegonia at the tip. (× 7)

forms spores. This sporogenous tissue is in the form of a hollow cylinder which surrounds a large columella (Fig. 818). Between the fertile region and the wall of the sporangium there is a region with very loose tissues and large air spaces. A considerable proportion of the capsule, including this loose tissue, contains chlorophyll and serves for assimilation (Fig. 818).

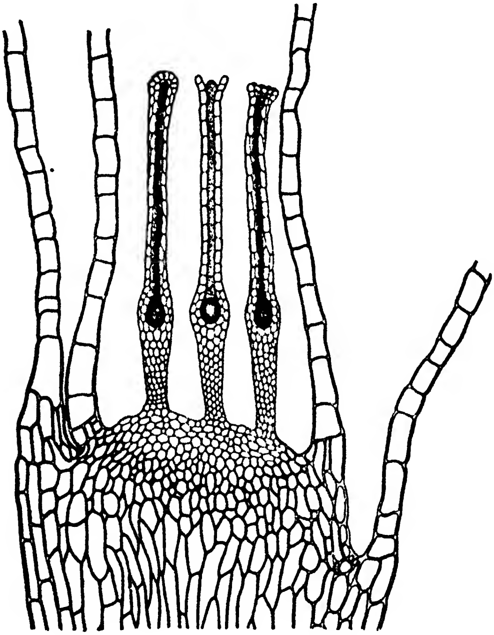


Fig. 816. Section through a tip of a moss plant, showing location of archegonia
The archegonium on the left has not yet opened; the one in the center is shown in section. (× 80)

The sporogenous tissue does not reach over the top of the columella as in *Sphagnum*. Instead, the upper part of the capsule is composed of rather small cells and is differentiated into two distinct structures. The upper part becomes a lid or operculum which is shed when the capsule is mature (Figs. 817, 818). Below this is the peristome, which slits into toothlike segments (Fig. 820) and thus makes an opening in the top of the capsule (Fig. 817).

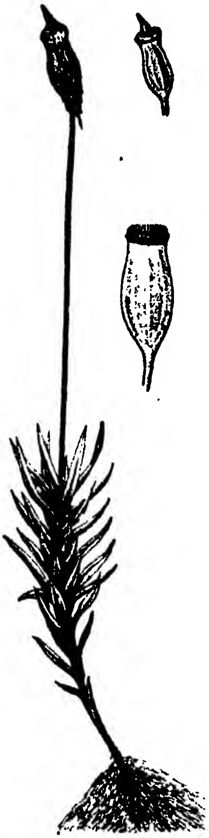


Fig. 817. Gametophyte and sporophyte of a moss

Left, a moss gametophyte bearing a sporophyte; note that the sporangium, or capsule, is covered by a hood, or calyptra, which was originally a part of the archegonium wall (× 1⅔). Upper right, a capsule with calyptra removed; the upper portion is differentiated into a lid, or operculum. Below this figure is shown a capsule with the operculum removed; note the fringe of toothlike appendages known as the peristome (× 3)

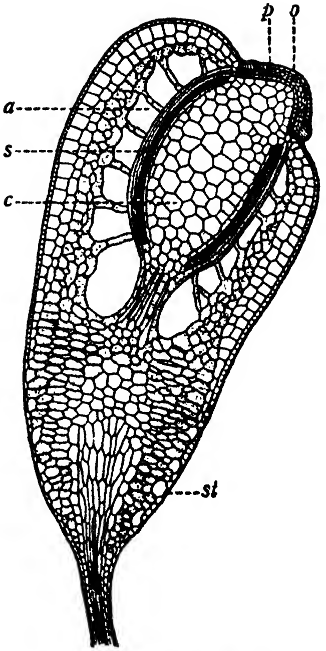


Fig. 818. Longitudinal section of capsule of *Funaria hygrometrica*

p, peristome; *o*, operculum; *a*, air space; *s*, spore-forming tissue; *c*, columella; *st*, stomata. The lightly shaded tissue contains chloroplasts and serves for photosynthesis. (Modified after Haberlandt)

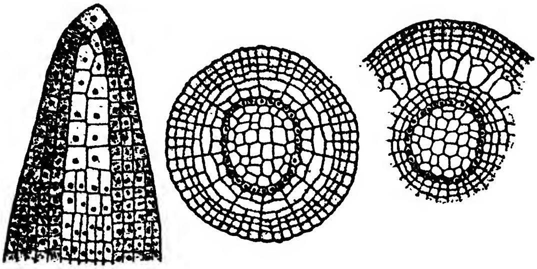


Fig. 819. Young sporangium of *Funaria*

Left, longitudinal section showing apical cell, which is necessary for the growth of the capsule. In having a sporophyte which grows by means of an apical cell the *Bryales* resemble the *Pteridophyta*. Center, cross section of sporangium. The cells in which the nuclei are shown compose the spore-producing tissue. Right, cross section of portion of sporangium at later stage, showing early stage in the formation of air spaces. (After Leclerc du Sablon)

Peristome. Usually the peristome is formed from a single layer of cells (Fig. 818). The upper and lower walls of this layer become greatly thickened, while the walls joining them are much thinner. The result is that there are two sheets of thick walls joined by thin walls. When the capsule ripens and dries, the peristome splits to form segments of much the same shape as the slices into which a pie is cut (Fig. 820). These segments are attached to the capsule by their broad bases and form the peristome teeth. As the upper and lower surface of each segment are composed of thick walls which are held together by thin walls, drying causes the upper and lower layer of each segment to split apart, thus forming a double layer of teeth.

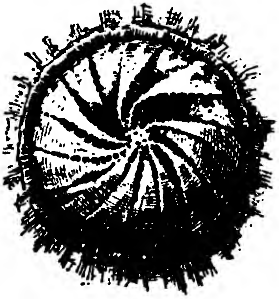


Fig. 820. Top view of peristome of a moss

Note that it is split into sections and that it is rough owing to projecting cell walls. (From Bergen and Caldwell, *Practical Botany*)

When the capsule is mature, the tissues in the neighborhood of the sporogenous region break down so that the spores occur in a loose powdery mass. The peristome teeth are hygroscopic, and are roughened by portions of cell walls which are attached to them. When they are wet or moistened by high humidity, they bend into the sporangia; when dry, they bend outward. In this way they seem to assist in the dissemination of spores, as they bring out spores when it is dry and the spores can be scattered by the wind.

Position of mosses in the plant kingdom. The mosses, as we have seen, appear to be descended from the liverworts. In them there has been a higher development of both gametophytes and sporophytes. The capsule of the latter has become highly specialized. That the specializations found in mosses have fitted them extremely well for the struggle for existence is indicated by the large number of species, and particularly by their wide distribution and the enormous number of individuals. However, they do not seem to have developed into anything higher than themselves. It is probable that while their high degree of specialization has fitted them for a very successful existence, it has made them unfitted for development along new lines.

CHAPTER XXVII

DIVISION *PTERIDOPHYTA* (FERNS AND FERN ALLIES)

General characteristics. The ferns are the commonest and best known of the living pteridophytes. Also common and well known are the lycopods or clubmosses, some of the terrestrial species of which are known as ground pines. A third common and familiar group comprises the horsetails or scouring rushes.

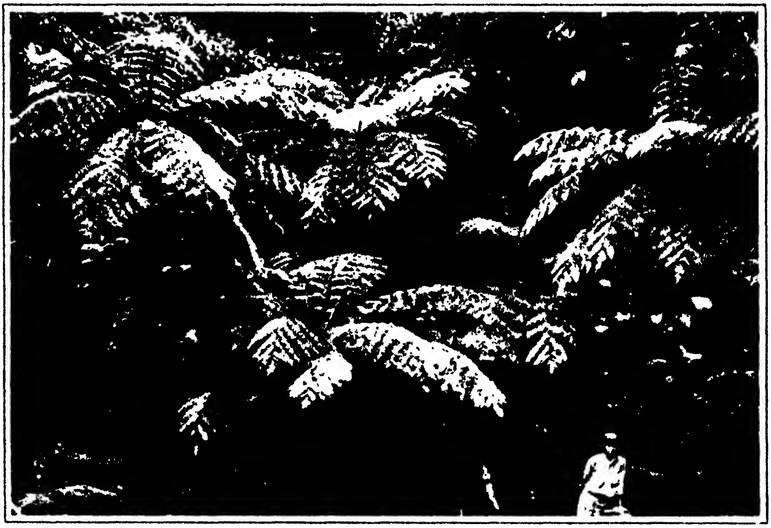


Fig. 821. A group of large tree ferns (*Cyathea*) in a mountain forest in the Philippines

In the *Pteridophyta* the sporophyte is the conspicuous and familiar plant, while the gametophyte is always small and inconspicuous. The gametophyte is in general much less developed, and is simpler, than that of the *Bryophyta*. The sporophyte is usually a large or relatively large plant, is differentiated into stems and leaves, and in nearly all cases has roots. In its early stages it is like

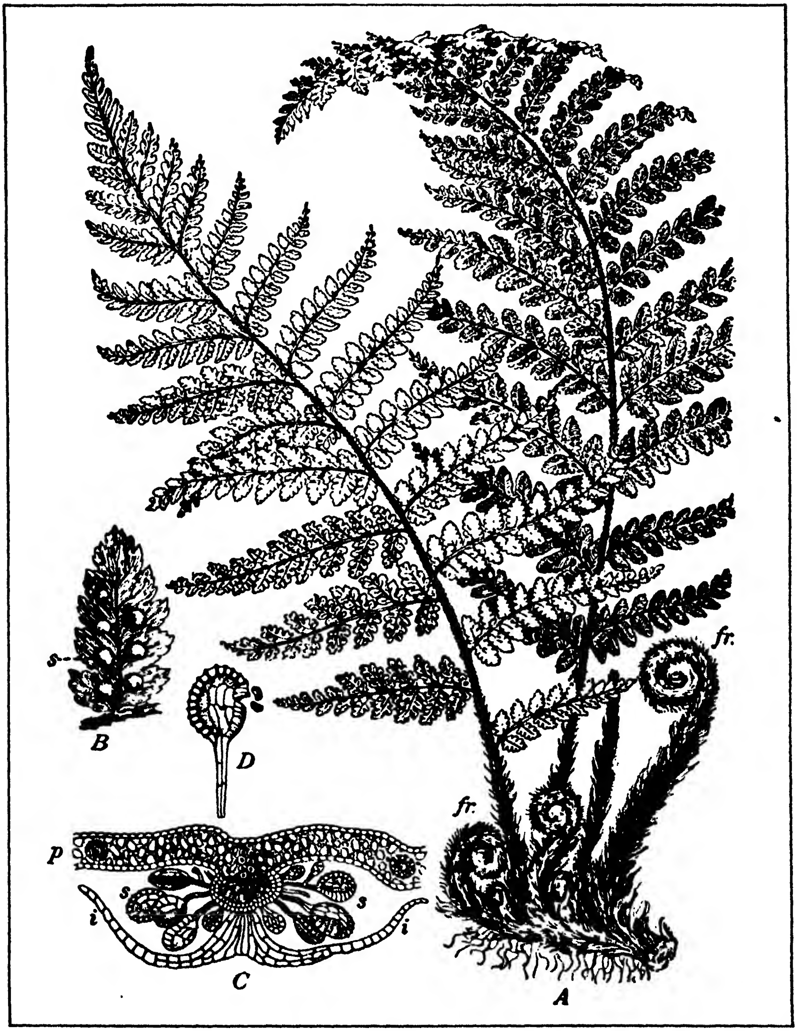


Fig. 822. Spore-plant of a fern (*Aspidium Filix-mas*)

A, part of rootstock and fronds, not quite one-sixth natural size; *fr*, young fronds unrolling (not usually found at the same season as the mature fronds). *B*, under side of a pinnule, showing sori *s*. *C*, section through a sorus at right angles to surface of leaf, showing indusium *i*, and sporangia *s*. *D*, a sporangium discharging spores. (*B* is not far from natural size. *C* and *D* are considerably magnified.) (After Wossidlo)

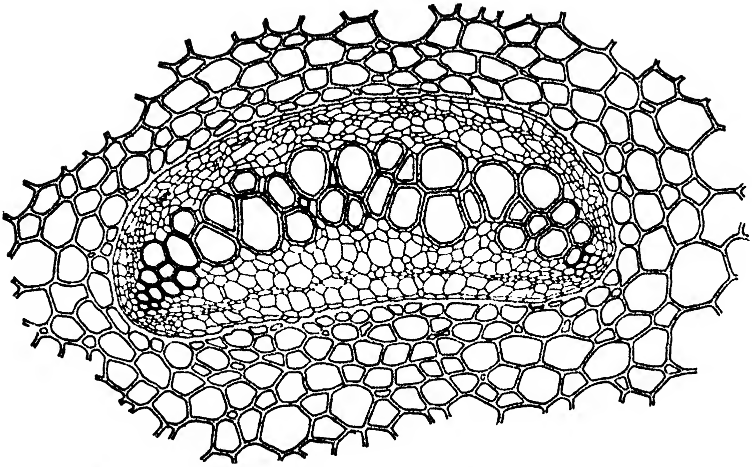


FIG. 823. Section of a concentric vascular bundle of a fern (*Davallia solida*) Note that the xylem is surrounded by the phloem. (× 110)

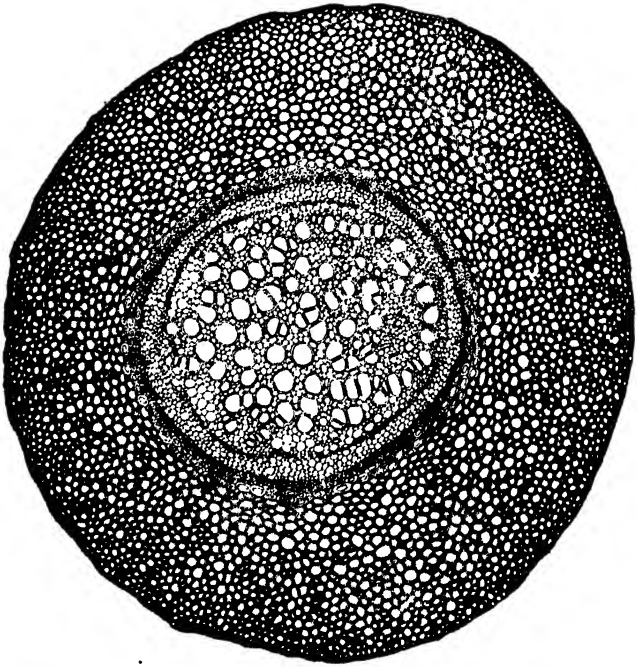


FIG. 824. Cross section of a fern stem (*Gleichenia*) showing protostele Note that the stele is solid and is concentric, that is, the xylem is surrounded by the phloem. Outside the stele is the cortex. (× 50)

the sporophyte of the *Bryophyta* in that it is attached to the gametophyte by a foot and is dependent on the gametophyte for nourishment. Soon, however, it develops its own stems, leaves, and roots, and becomes independent of the gametophyte, which goes to pieces and disappears. The sporophytes are long-lived plants, and, in addition to their vegetative organs, produce large numbers of sporangia. As ferns are the commonest of the pteridophytes and as their life history is easily observed and studied, the experimental cultivation of many species being comparatively easy, the typical life history of a fern affords an excellent type for the study of *Pteridophyta.*

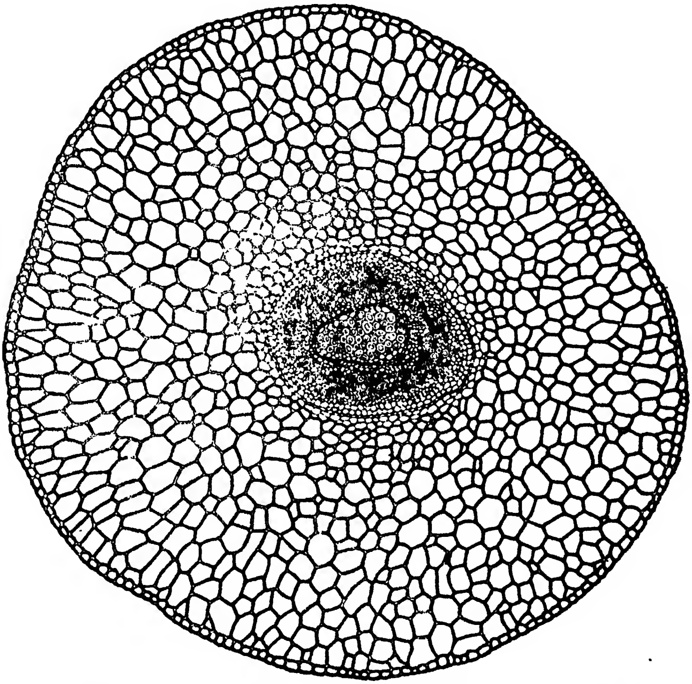


FIG. 825. Section of a stem of a maidenhair fern (*Adiantum*), showing a siphonostele

Note that there is a central pith composed largely of thick-walled sclerenchyma cells, and that outside the stele is a wide cortex. The xylem is bordered on both sides by phloem. (× 35)

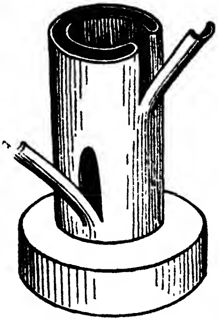


Fig. 826. Diagram of a siphonostele of a fern, showing leaf gaps where leaf traces leave the stele

Sporophyte of a fern. The sporophyte of ferns (Fig. 821) varies greatly in size, ranging from small mosslike species to the tall tree ferns. The structure and appearance also vary greatly in different cases. The sporophyte of typical ferns has a fair-sized stem, a few large leaves (Fig. 822), and numerous roots. A very characteristic feature of ferns is the manner in which the young leaves are coiled circinately (Figs. 822, 828).

The ferns have highly developed vascular bundles. The characteristic type in the stems of ferns is concentric

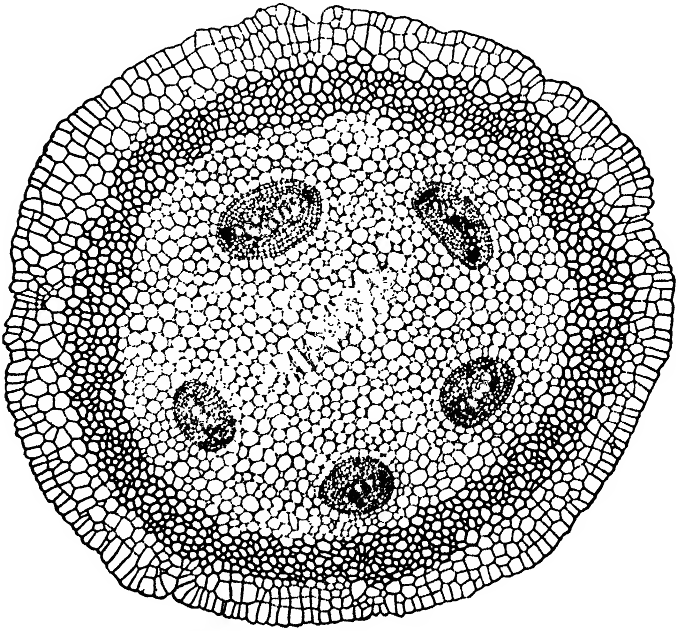


Fig. 827. Cross section of stele of a fern (*Cyclophorus adnascens*), in which leaf gaps are so long that there appear to be five separate bundles in the stele

Note the sclerenchyma in the center of the stele and also the cylinder of sclerenchyma near the outside of the cortex. (× 50)

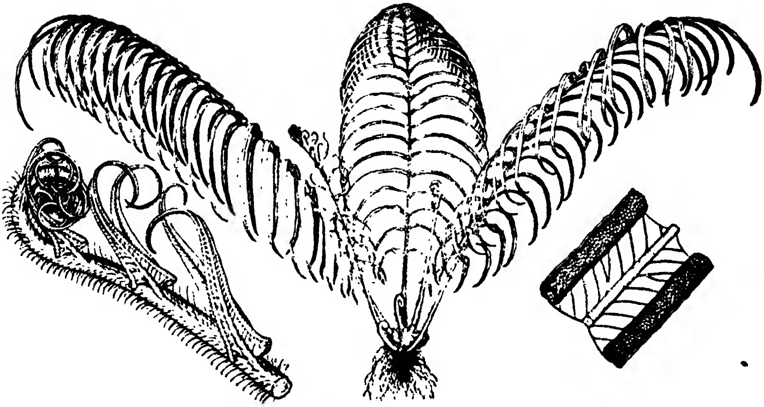


FIG. 828. Sporophyte of *Pteris longifolia* (× $\frac{1}{10}$)

On the left is the tip of a young leaf which is unrolling (× 1); on the right, the under surface of a fertile pinna, showing sporangia aggregated near the sides (× 2)

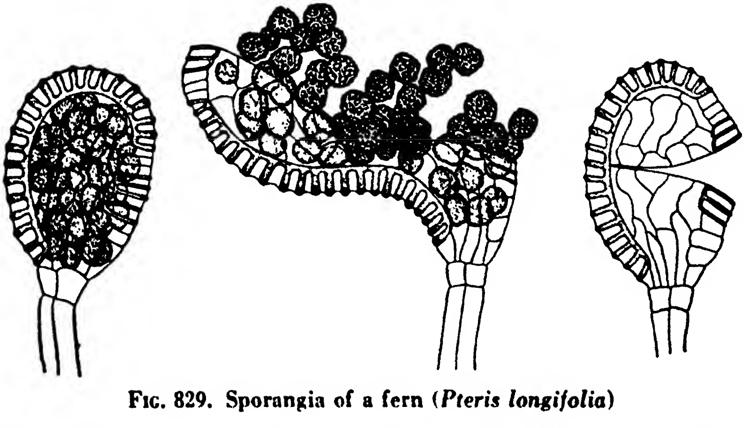


FIG. 829. Sporangia of a fern (*Pteris longifolia*)

Left, entire sporangium; center, sporangium opened by the bending back of the annulus (the row of thick-walled cells); right, the annulus has returned to its original position, which movement resulted in the scattering of the spores. (× 85)

(Fig. 823), the xylem being surrounded by phloem. The most primitive type of stele is a protostele (Fig. 824), or solid stele, in which there is no pith within the vascular system. A more advanced type is the siphonostele (Fig. 825), in which the vascular system is in the form of a cylinder that encloses a central pith; where a bundle that supplies a leaf leaves the siphonostele, an opening, or leaf gap (Fig. 826), occurs in the cylinder above the place of origin of the leaf bundle. When these gaps are greatly elongated and extend through several nodes the cylinder consists of a coarse mesh, and in cross section the stele appears to be composed of a number of separate bundles (Fig. 827); such a type of stele is merely a modification of a simple siphonostele, but is frequently called a polystele. It may be further complicated by the formation of extra bundles which develop as branches from the original cylinder.

In primitive siphonosteles the xylem is bordered by phloem both toward the center and toward the exterior (Fig. 825). In certain more advanced types there is no internal phloem. The steles of modern conifers and dicotyledons appear to have been derived from a siphonostele from which the internal phloem has disappeared and in which there has been a massive development of secondary xylem.

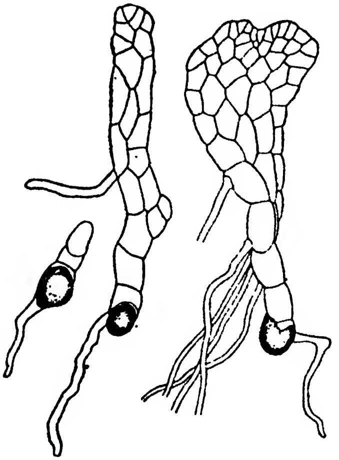


Fig. 830. Germination of fern spore and early stages in growth of prothalli

The sporangia of ferns are usually borne on the lower surfaces of the leaves (Figs. 822, 828) and are aggregated in definite areas, the sori. In each sporangium there are many spores (Fig. 829). As in the *Bryophyta*, a large number of spore mother cells are produced in a sporangium. Each mother cell divides to form a tetrad of spores. When a spore germinates (Fig. 830) it produces a small green thallus, the gametophyte (Fig. 831).

✓ **Gametophyte of a fern.** The gametophyte of the ferns is known as the prothallus (Fig. 831). It is typically a delicate, thin,

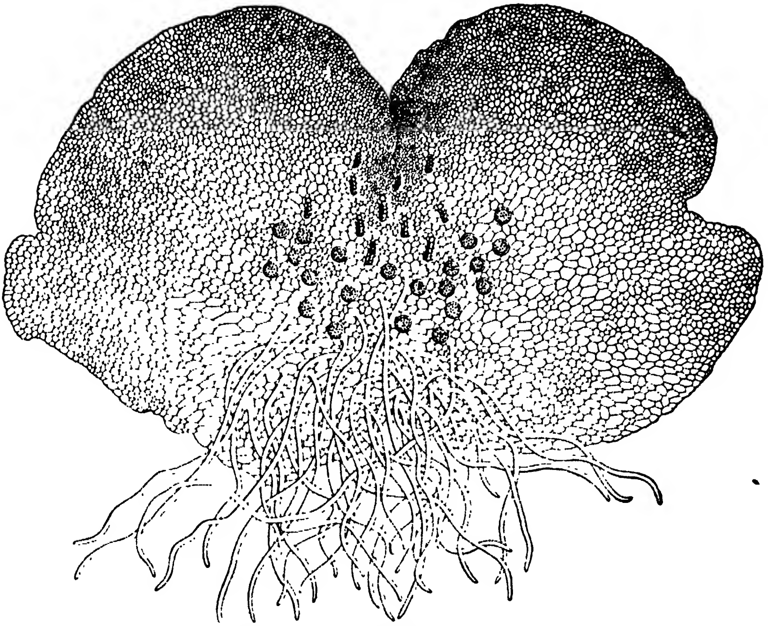


Fig. 831. Lower surface of prothallus, or gametophyte, of a fern

Near the base of the prothallus are numerous rhizoids; in the center are rounded antheridia containing spermatozoids; near the apex are archegonia which point toward the base

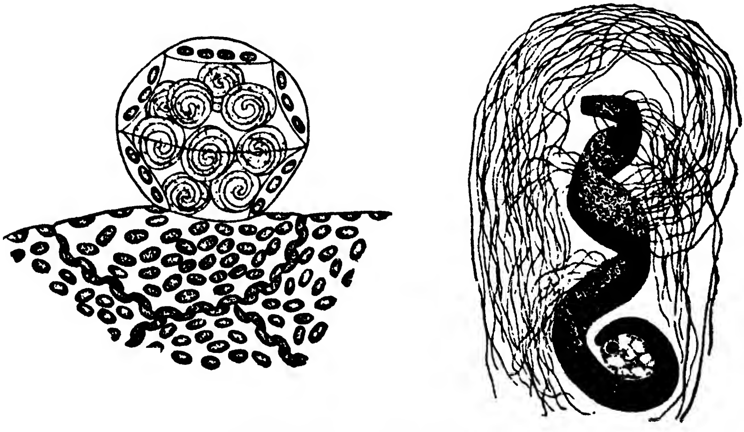


Fig. 832. Antheridium of a fern

Left, an antheridium on the side of a prothallus of a fern; note the coiled spermatozoids within the antheridium (× 845). Right, a single spermatozoid of a fern. (Spermatozoid after Yamanouchi) expanded thallus which is attached to the ground by numerous rhizoids. The latter are slender filaments which absorb water and mineral matter just as do the root hairs of flowering plants. The typical prothallus of a fern is an independent plant which manufactures its food by means of its chloroplasts and absorbs water through its rhizoids. Usually a prothallus bears both archegonia and antheridia (Fig. 831), but in some cases the antheridia and archegonia are borne on different prothalli. The antheridia (Figs. 832, 833) are spherical and contain numerous spermatozoids. The spermatozoid (Fig. 832) is a spiral structure, toward one end of which are numerous flagella which enable it to swim through water. As in the *Bryales*, an archegonium is a flask-shaped structure. In the enlarged basal portion, or venter, there is a large egg (Fig. 834), and exterior to this a smaller cell, the ventral canal cell. In the neck of typical ferns there are two neck canal cells. When the archegonium matures, the ventral canal cell and neck canal cells become disorganized, and the apical wall cells of the neck spread apart enough to leave an opening (Fig. 835), so that there is a passage through which the sperm can reach the egg. The archegonia of the *Pteridophyta* are in general like those of the *Bryophyta*.

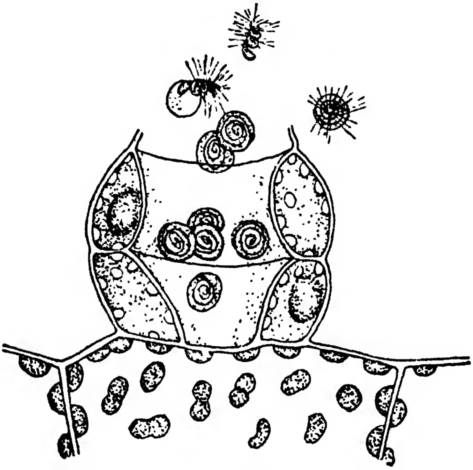


FIG. 833. A fern antheridium from which the spermatozoids are escaping
After Luerssen; from Bergen and Caldwell, *Practical Botany*

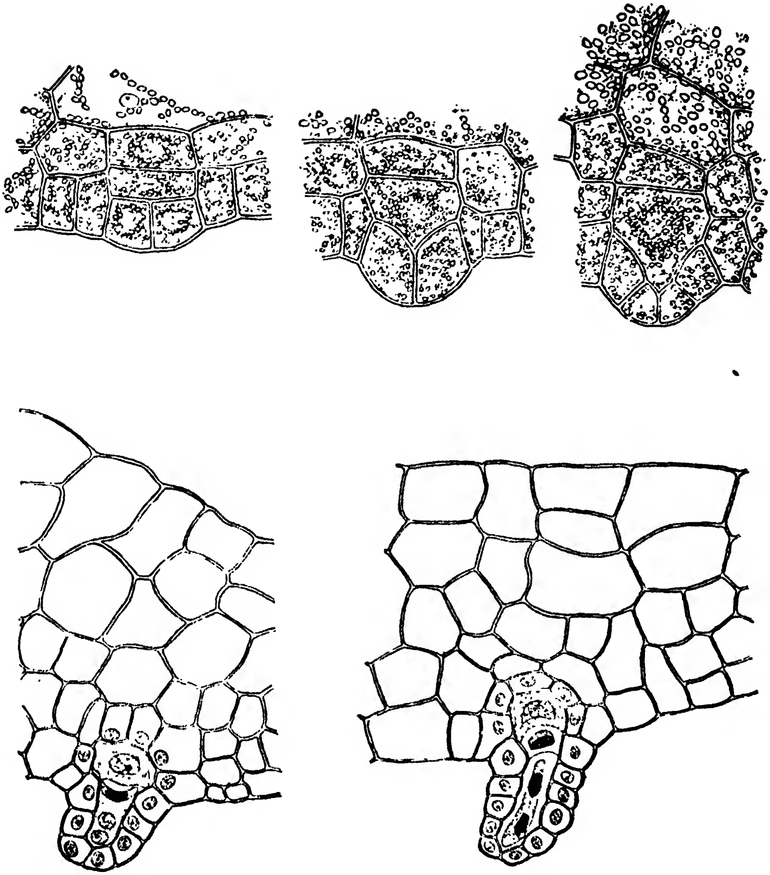


Fig. 834. Development of a fern archegonium

Above, early stages. (After Kny.) Below: at left, the enlarged base, or venter, contains an egg, and exterior to this is the ventral canal cell, while in the neck are two neck canal cells; at right, the ventral canal cell and neck canal cells have begun to disorganize (× 185)

They differ from the archegonia of the *Bryophyta*, however, as they are much shorter and are without stalks, and the base is usually within the prothallus. A spermatozoid swims from an antheridium and enters an archegonium (Fig. 836) to which it is attracted by a chemical stimulus. One spermatozoid fuses with the egg (Fig. 836). As in the case of the *Bryophyta*, water is necessary to accomplish fertilization, because the spermatozoid has no way of reaching the archegonium except by swimming.

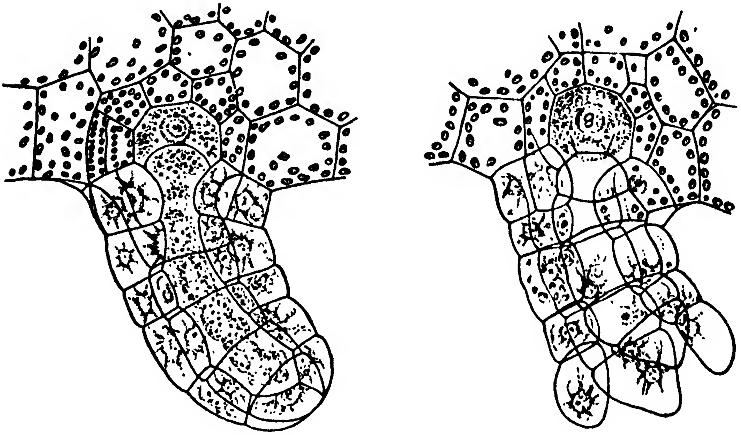


FIG. 835. Archegonia of a fern

Left, the neck canal cells and ventral canal cell are disorganized, but the archegonium has not opened; right, archegonium open. (Redrawn after Strasburger)

Development of sporophyte. The fertilized egg develops at once into a sporophyte (Fig. 837). During the early stages of its growth the sporophyte is dependent on the prothallus for nourishment. The fertilized egg divides into four segments, one of which develops into a foot, which absorbs nourishment from the prothallus. Of the other three cells, one typically produces the stem, one a root, and one the first leaf. Like the foot, the first root and the first leaf are transitory structures, the whole of a mature sporophyte being derived from the original stem cell. The young embryo soon produces a stem, roots, and leaves, and thus becomes independent of the gametophyte. After such development has occurred, the gametophyte is consumed or dies and the sporophyte

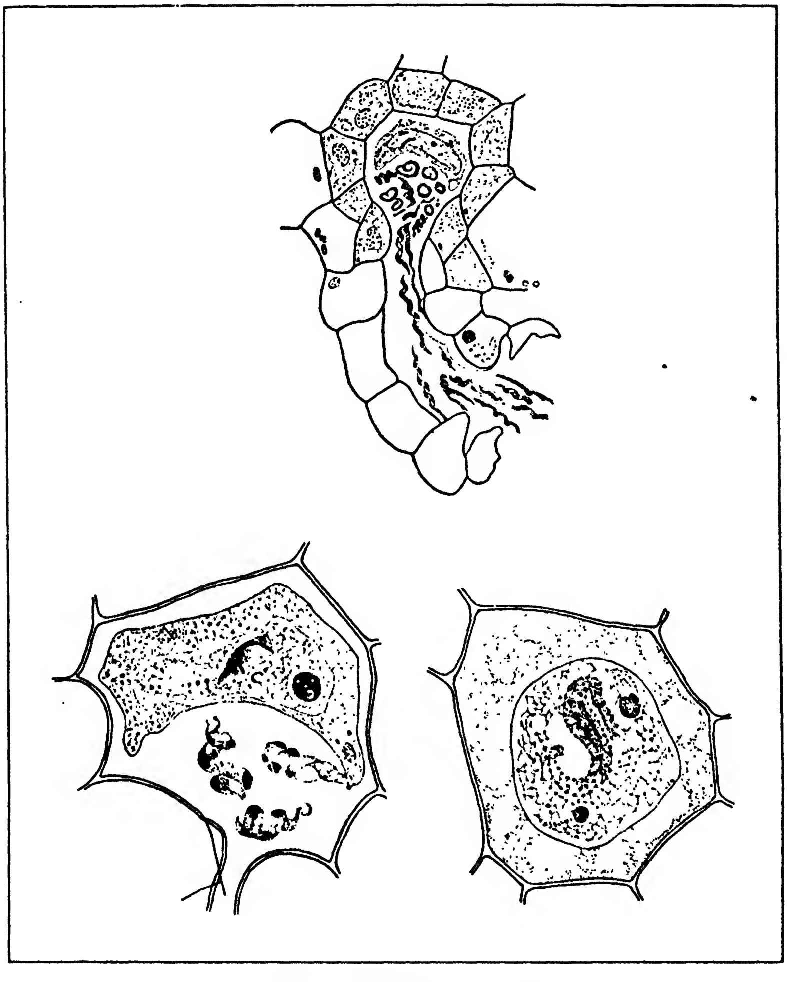


Fig. 836. Fertilization in a fern

Above, spermatozoids are entering neck of archegonium; lower left, vertical section through venter, showing a single spermatozoid in the nucleus of the egg; lower right, horizontal section through venter, showing a later stage in the union of spermatozoid and egg nucleus. (Redrawn after Shaw) continues to live independently. Thus in a typical fern (Fig. 838) the sporophyte and the gametophyte are independent plants.

Alternation of generations. As in the *Bryophyta,* the cells of the gametophyte are haploid and those of the sporophyte diploid. Again as in the *Bryophyta,* the spores are formed in tetrads (groups of four) by two successive divisions of each spore mother cell. The reduction in the number of chromosomes occurs in these two divisions; the double number is restored when an egg is fertilized by a spermatozoid. Therefore the ferns resemble the bryophytes in having an alternation of generations consisting of a haploid gametophyte and a diploid sporophyte. As in the *Bryophyta,* the sporophyte starts with the fertilized egg and ends with the spore mother cell, while the gametophyte begins with the spore.

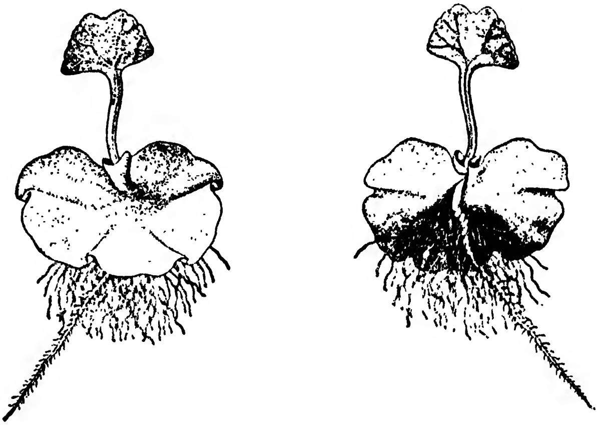


FIG. 837. Prothallus of a fern with young sporophyte attached

Left, as seen from above; right, as seen from below. (× 3½)

Classes of *Pteridophyta.* The *Pteridophyta* are a very ancient stock, dating back to Devonian times. They have developed along very distinct lines and may be divided into four classes: ***Psilophytineae,*** an extinct Devonian class; ***Equisetineae*** (horsetails); ***Lycopodiineae*** (clubmosses); and ***Filicineae*** (ferns).

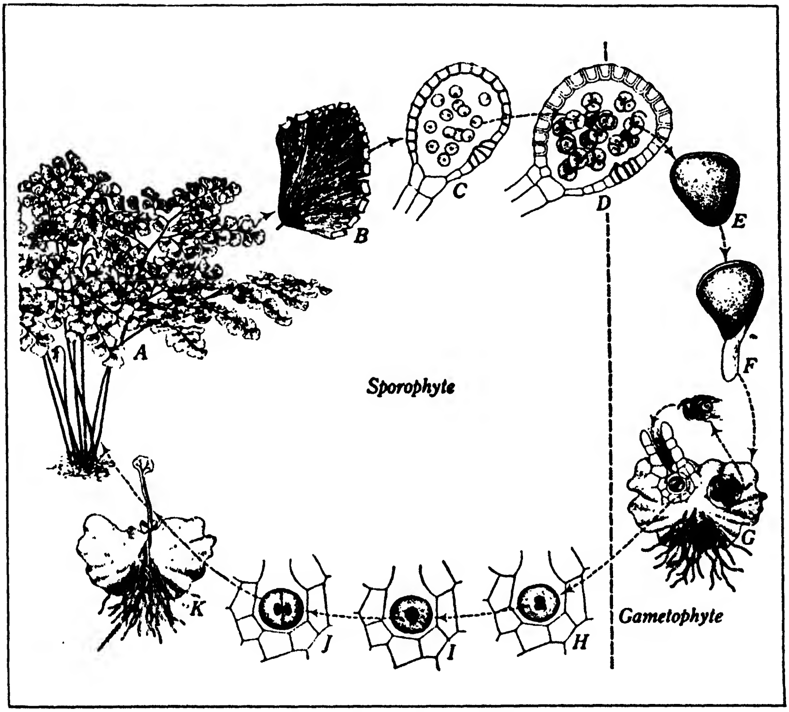


Fig. 838. Life cycle of a fern

A, sporophyte; *B*, pinnule of sporophyte; *C*, sporangium with spore mother cells; *D*, sporangium with tetrads of spores. The line separating the sporophyte and gametophyte is drawn through the sporangium, as a sporangium is part of the sporophyte while a spore is a first stage of a gametophyte. *E*, spore; *F*, spore beginning to germinate; *G*, prothallus produced from spore (a spermatozoid from the antheridium is represented as entering the archegonium to fuse with the egg); *H*, fertilized egg with egg and sperm nuclei in contact; the fertilized egg is a beginning of the sporophyte. *I*, egg and sperm nuclei have fused; *J*, two-cell stage of embryo; *K*, embryo still attached to prothallus

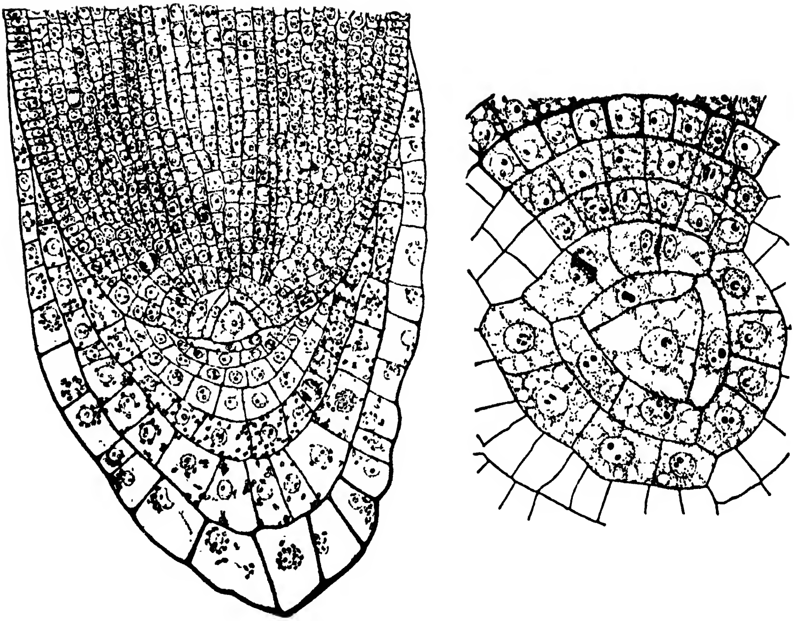


Fig. 839. Root tip of *Pteris gigantea*

Left, longitudinal section (near the center is the apical cell); right, cross section, showing apical cell. The apical cell is four-sided, one side being in contact with the root cap; longitudinal and cross sections appear, therefore, to be triangular. It cuts off segments on all four sides: the segments formed toward the root cap form root-cap cells; those cut off toward the root divide up, as shown, to form the tissues of the root. (After Hof)

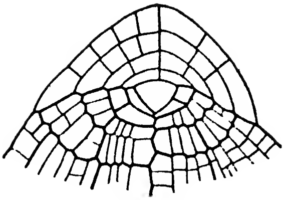


Fig. 840. A somewhat diagrammatic representation of the apical region of the root of a fern

In the center is the apical cell, which in section appears triangular but which in reality is four-sided. Segments cut off from the apical side form the root cap. Those below form the root. Regions enclosed by heavy lines are derived from a subdivision of a segment of the apical cell. (Redrawn after Naegeli and Leitgeb from Sachs)

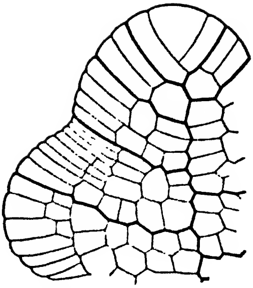


Fig. 841. Portion of a young leaf of a fern, *Ceratopteris*, showing apical growth

Redrawn after Kny from Sachs

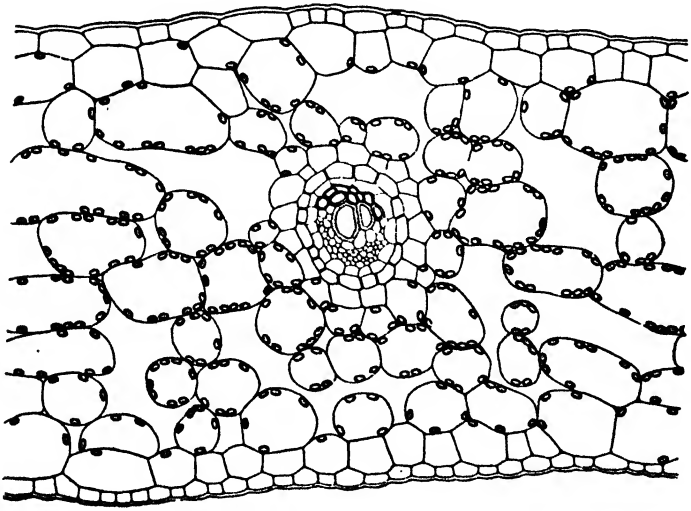


Fig. 842. Cross section of a fern leaf. (× 240)

CLASS *PSILOPHYTINEAE*

Order *Psilophytales*

General characteristics. The most ancient of known land plants appeared in the early Devonian. They belonged to an extinct order (*Psilophytales*), widely regarded as the most primitive order of the *Pteridophyta.* They get their name from *Psilophyton* (Fig. 850), the first-described genus. While they were distinctly land plants, the simple forms of some of the genera have been regarded by many authorities as showing considerable resemblance to algae.

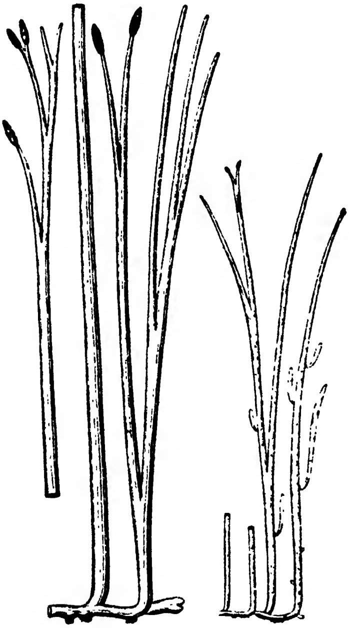


Fig. 843. ***Rhynia***

Left, *Rhynia major* (× ⅓); right, *Rhynia Gwynne-Vaughani* (× ⅓). Note the sporangia at the ends of the branches. (After Kidston and Lang)

The *Psilophytales* had dichotomously branched, cylindrical aerial branches that grew from underground rhizomes. In most cases the branches were leafless (Fig. 843), but in one genus there were small spirally arranged leaves (Figs. 851, 852). The young parts of the branches of some genera were coiled circinately as are the leaves of ferns (Figs. 850, 852). There were no roots, but in some genera the rhizomes bore rhizoids. The branches had a vascular system surrounded by a cortex, this in turn being surrounded by an epidermis (Fig. 844) with typical stomata (Fig. 855). The vascular system consisted of tracheids surrounded by phloem (Fig. 845).

The *Psilophytales* had sporangia which terminated the aerial branches and, at least in some cases, were hardly more than modified branch ends (Figs. 846, 847). The spores were in tetrads as in the other *Pteridophyta* (Fig. 848).

Rhynia. The plants of the genus *Rhynia* had upright, slender, cylindrical leafless aerial stems which grew from underground stems or rhizomes to a height of twenty centimeters or more and which occasionally branched dichotomously (Fig. 843). They had no roots, but numerous rhizoids grew from the rhizomes.

The stem contained a very simple vascular system consisting of xylem composed of annular tracheids and surrounded by phloem (Figs. 844, 845). Around the vascular system was a wide cortex surrounded by an epidermis with scattered stomata.

The sporangia were cylindrical structures which terminated aerial branches. They contained numerous spores, which are sometimes found still grouped in tetrads (Figs. 846, 847). Between the spore cavity and the epidermis were a number of layers of small thin-walled cells.

Hornea. The aerial stems of *Hornea* were rather similar to those of *Rhynia*. The rhizomes had tuberous enlargements which bore rhizoids and from which the aerial stems grew (Fig. 849). The sporangia differed from those of *Rhynia*

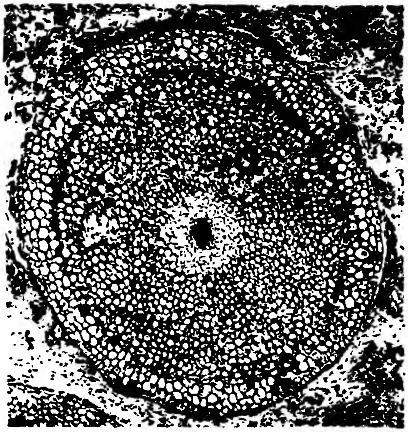


Fig. 844. Cross section of stem of *Rhynia major*

The small dark area in the center is the xylem. The light area with small cells around this is the phloem. Between the phloem and the epidermis is the cortex, which is differentiated into an inner and an outer region. (× 11). After Kidston and Lang

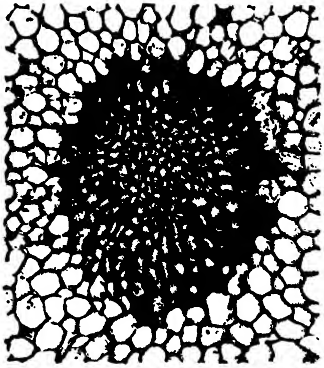


Fig. 845. Cross section of xylem and portion of the phloem of *Rhynia major*. (× 60)

After Kidston and Lang

in that the spore cavity was dome-shaped and extended around and over a sterile region or columella as in *Anthoceros* (Fig. 848).

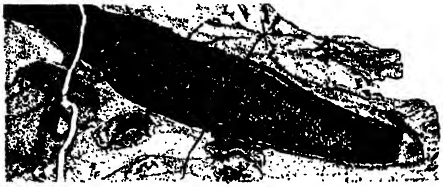


Fig. 846. Longitudinal section of sporangium of *Rhynia major.* (× 3½)

After Kidston and Lang

Psilophyton. This genus resembles *Rhynia* in many respects. It had underground rhizomes with rootlike branches, and erect leafless stems which branched dichotomously (Fig. 850). The tips of the branches were coiled circinately, in which respect they resembled the young leaves of ferns. In fact, an aerial stem of *Psilophyton* with its dichotomous branching and its circinately coiled tips suggests a fern frond without a lamina. This resemblance is emphasized, at least superficially, by the probability that the fronds of the most ancient of the fern line consisted of branched rachises with little or no lamina.

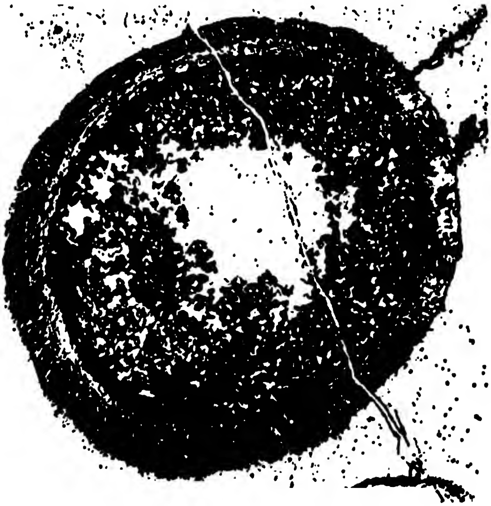


Fig. 847. A cross section of sporangium of *Rhynia major.* (× 14)

After Kidston and Lang

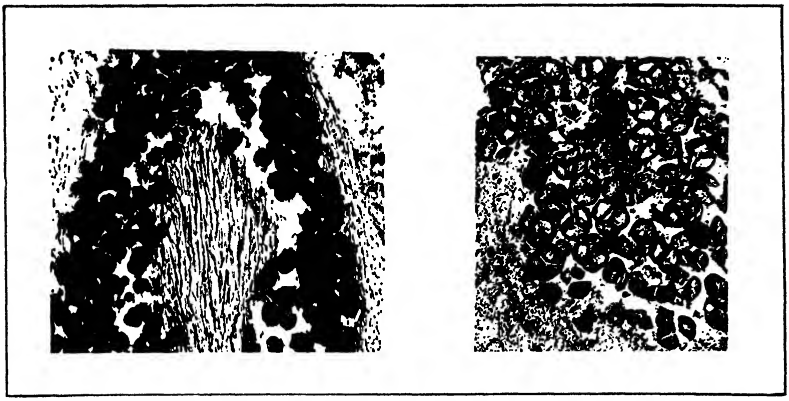


Fig. 848. *Hornea*

Left, spores around sterile columella (× 40); right, spores in tetrads (× 70). (After Kidston and Lang)

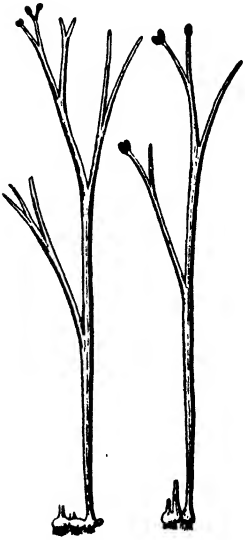


Fig. 849. *Hornea lignieri*

Note the sporangia at the tips of branches. (× ½). After Kidston and Lang

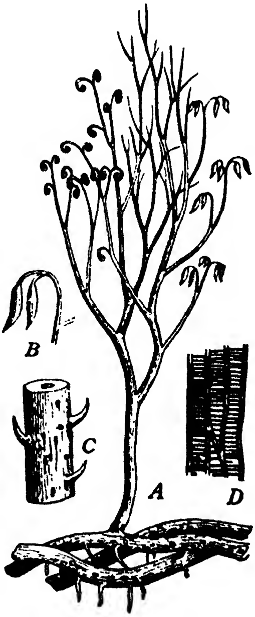


Fig. 850. *Psilophyton princeps*

A, a plant, showing young branches uncurling at the left and branches bearing sporangia at the right; *B*, tip of a branch with two sporangia; *C*, lower part of a stem, showing thorns; *D*, longitudinal section of xylem. (After Dawson)

The sporangia were large oval structures, borne in pairs at the tips of the stems.

Asteroxylon. This genus had a more complex structure than those previously described. The aerial branches grew from cylindrical, dichotomously branched rhizomes which behaved in a rootlike manner (Figs. 851, 852). The anatomy of the rhizome was similar to that of *Rhynia,* but there were no rhizoids.

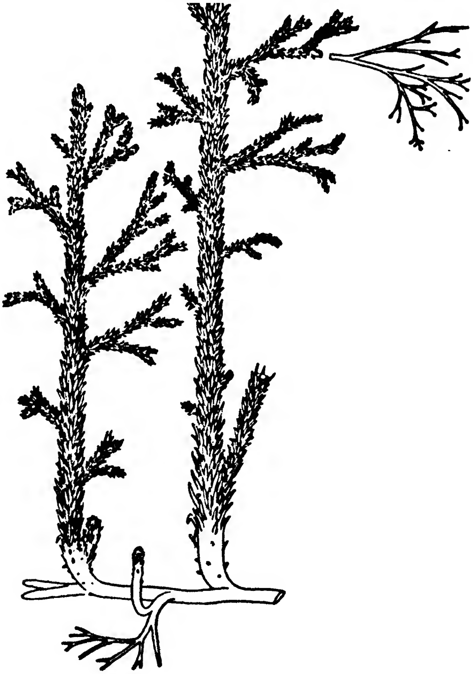


FIG. 851. ***Asteroxylon mackiei***

Note sporangia-bearing branch to the right. (× ½). After Kidston and Lang

The aerial branches were dichotomously branched and somewhat thickly clothed with small spirally arranged leaves. The leaves were about half a centimeter in length and oval in transverse section. They were without veins, the leaf trace or bundle ending in the base of the leaf.

The xylem of the leafy branches was star-shaped, with phloem completely surrounding the xylem (Figs. 853, 854).

The sporangia of *Asteroxylon* were pear-shaped and dehisced apically. They terminated leafless branches.

Just as *Psilophyton* has some fernlike characteristics, so *Asteroxylon* is suggestive of a lycopod.

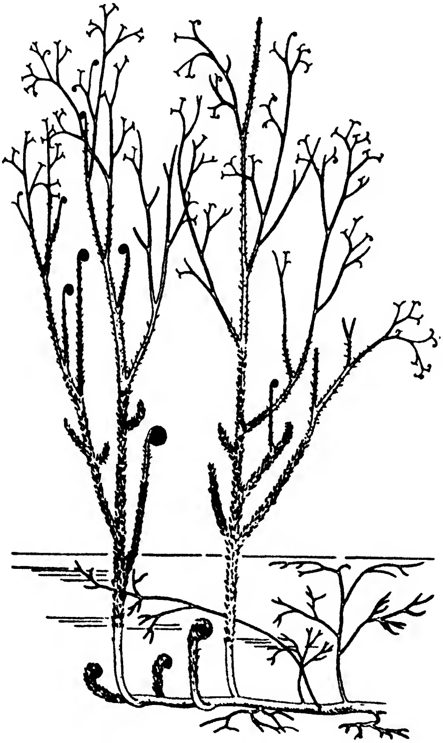


Fig. 852. ***Asteroxylon eberfeldense***

Note rootlike branches below the soil and coiled tips of aerial branches. (After Krausel and Weyland)

Occurrence of *Psilophytales*. *Psilophytales* have been found in Devonian strata in various parts of the world, but fossils with well-preserved internal structure are known only from one place near the village of Rhynie in Aberdeenshire, Scotland. Here there was a swamp in early Devonian times, and also a mineral spring or some other source of water with a high percentage of silica, and so the remains of the plants which grew in the swamp were impregnated with silica. This material has given very complete information on the structure of some of the *Psilophytales* and has been of great help in interpreting fossils found elsewhere. Further knowledge may show that other types of plants lived in the lower Devonian.

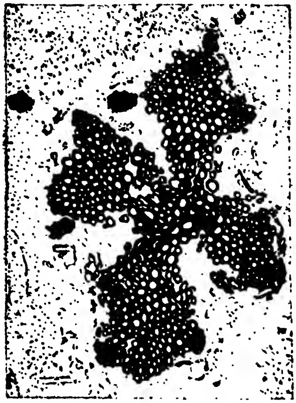


Fig. 853. Cross section of xylem of *Asteroxylon mackiei.* (× 44)

After Kidston and Lang

Relationship of *Psilophytales.* The *Psilophytales* contain the most simply organized of the *Pteridophyta* and the most ancient known forms of this group. They appear to represent the ancestral stock of the *Pteridophyta.* The dichotomous branching characteristic of the *Psilophytales*, the prevailing concentric protostele, and the circinately coiled stems of some species are suggestive of primitive ferns. The lack of a lamina in most species is in keeping with this view, as a naked rachis without a lamina appears to be more primitive in the fern stock than the possession of a lamina. While the sporophyte of the *Psilophytales* is much more developed than that of any bryophyte, it is relatively simple as compared with that of most *Pteridophyta*, and has not developed roots, which are so characteristic of most *Pteridophyta* and all higher plants. The relationship of the *Psilophytales* to the various orders of the *Pteridophyta* will be discussed later.

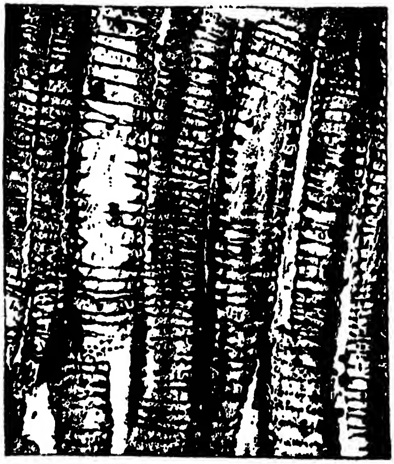


Fig. 854. Longitudinal section of xylem of *Asteroxylon mackiei.* (× 180)

After Kidston and Lang

The structure of the *Psilophytales* fits in very well with the long-accepted idea that the *Pteridophyta* are derived from the *Bryophyta.* The cylindrical stems of the simpler *Psilophytales* with their typical stomata are very suggestive of the sporophyte of the *Anthocerotales.* The similarity in the way in which the sporogenous tissues of the sporophytes of both *Hornea* (Fig. 848) and a young *Anthoceros* (Fig. 805) surround and overarch a sterile columella is particularly suggestive. We have no knowledge as to the gametophytes of the *Psilophytales,* but it is rather easy to imagine that the sporophytes of the simpler forms are a highly developed and branched development from some sporophyte similar to that of *Anthoceros.*

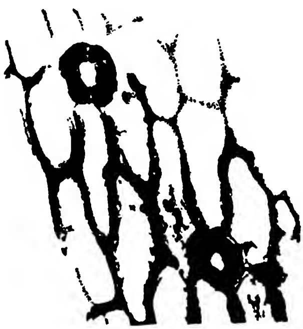


Fig. 855. Stomata and epidermis of *Asteroxylon mackiei.* (× 120)

After Kidston and Lang

Some paleobotanists have taken a different view, because the *Psilophytales* antedate any remains which can be positively assigned to the *Bryophyta.* They have seen in the simple *Psilophytales* a resemblance to an algal thallus, and believe that the *Psilophytales* represent a modification of such a thallus. Against this point of view it may be said that the *Psilophytales* are very typical land plants with well-developed supporting and conducting tissue, typical stomata, and a cutinized epidermis. All of these features argue for a long terrestrial ancestry and are in conformity with the derivation of the *Psilophytales* from the liverworts. That liverworts have not been found in the earliest rocks is explained in part by their delicate structure; and it may be that, like the ferns, they were by no means so abundant in ancient times as at present. For a long time liverworts were not known from the Paleozoic; but the finding of typical, highly developed, and highly differentiated liverworts in the Carboniferous shows that at that time they existed in much the same form as at present, and so must have had a long history. This information has gone a long way toward removing objections against a liverwort ancestry for the *Pteridophyta.*

Psilotales, Relics of the Devonian Period

Many of the groups of plants which were prominent and important in the past are represented by survivors in the present flora, and so the question naturally arises as to whether or not there are living representatives of the *Psilophytales.* In this connection the *Psilotales* are most interesting.

This order is composed of two small genera, *Psilotum* (Fig. 856), which occurs in tropical and subtropical regions, and *Tmesipteris* (Fig. 857), which is found from the southern Philippines to New Zealand and in parts of Polynesia. Both genera resemble the *Psilophytales* in lacking roots. In them, as in *Asteroxylon*, branched rootlike rhizomes take the place of roots.

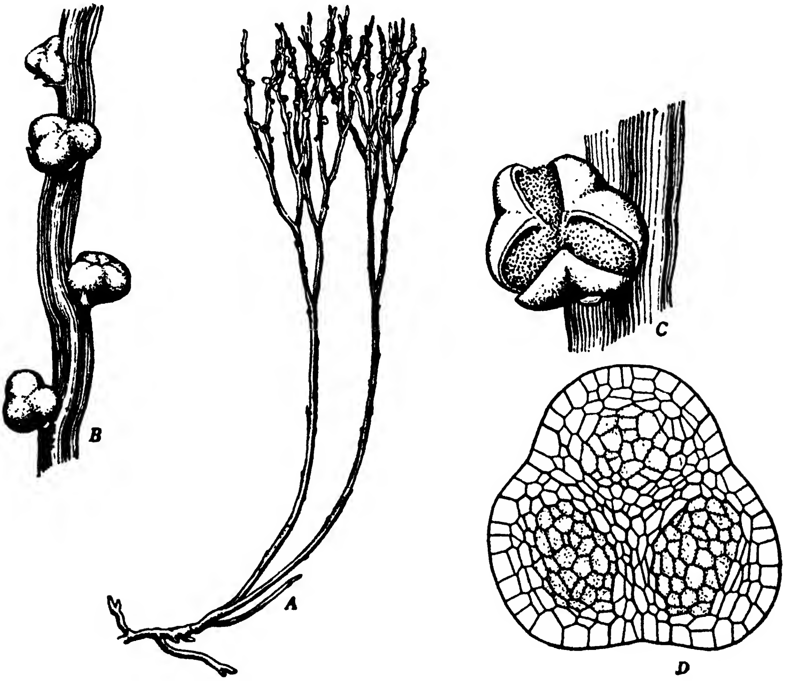


Fig. 856. ***Psilotum triquetrum***

A, habit (× ½). *B*, branch with sporangia. *C*, a single sporangium. *D*, cross section of a young sporangium; the shaded cells are the spore-producing tissues. (*D*, after Bower)

The aerial shoots, as in the *Psilophytales*, branch dichotomously (Fig. 856). *Tmesipteris* is usually unbranched. The leaves are spirally arranged. Those of *Psilotum* are scalelike, while those of *Tmesipteris* are longer. The sporangia are borne on the upper surfaces near the bases of leaves called sporophylls. In *Psilotum* the sporangia contain three chambers (Fig. 856), in *Tmesipteris* two (Fig. 857). Some authorities regard the sporangia as modified branches, which are in the axils of the leaves and which are terminated by the sporangia. This theory would give the sporangia a terminal position as in the *Psilophytales.*

The anatomy of the stem is very simple and shows primitive features. Altogether it is very suggestive of *Asteroxylon.*

The prothalli are small and colorless, and live saprophytically within the substratum in connection with fungi (mycorrhiza). They bear numerous archegonia and antheridia (Fig. 858). The spermatozoids are multiflagellate as in ferns. Dependence on mycorrhiza for nutrition would not appear to be a primitive feature, and yet it is interesting to note that this condition is found in the simplest of the living ferns and also in *Lycopodium.*

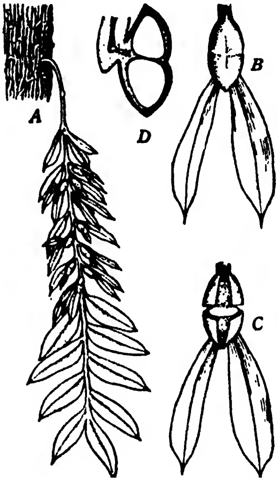


FIG. 857. ***Tmesipteris tannenis***

A, habit (× ½); *B*, enlarged view of sporangium; *C*, open sporangium (note the partition between the upper and lower sections); *D*, section of sporangium. (*D*, after Bower)

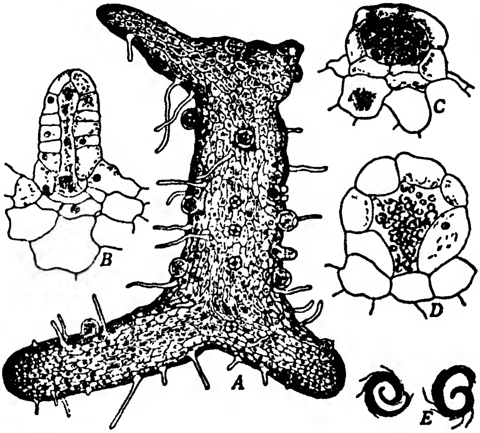


FIG. 858. ***Psilotum triquetrum***

A, an entire gametophyte with archegonia and antheridia; the archegonia can be distinguished by the prominent neck cells; four archegonia form an almost vertical line in the lower part of the center of the prothallus; the antheridia are rounded and appear larger than the archegonia. *B*, an archegonium. *C*, a young antheridium. *D*, a mature antheridium with spermatozoids. *E*, spermatozoids. (After Lawson)

The *Psilotales* show such a combination of primitive characters as is not found in any other group of living *Pteridophyta.* However, they have characters which for a long time caused them to be placed among the lycopods. A further study of the details of their structure led many authorities to believe that they were closely related to a relatively primitive group of *Equisetineae*, the *Sphenophyllaceae*, which had its origin in the Devonian period. Some leading authorities have also seen a relationship between the *Psilotales* and the simplest of living ferns. Altogether they seem to be a group which should be placed among the *Psilophytales* or close to them, and which can be regarded as a remnant of a flora that flourished in the mid-Devonian period before the more modern and specialized groups of the *Pteridophyta* had appeared.

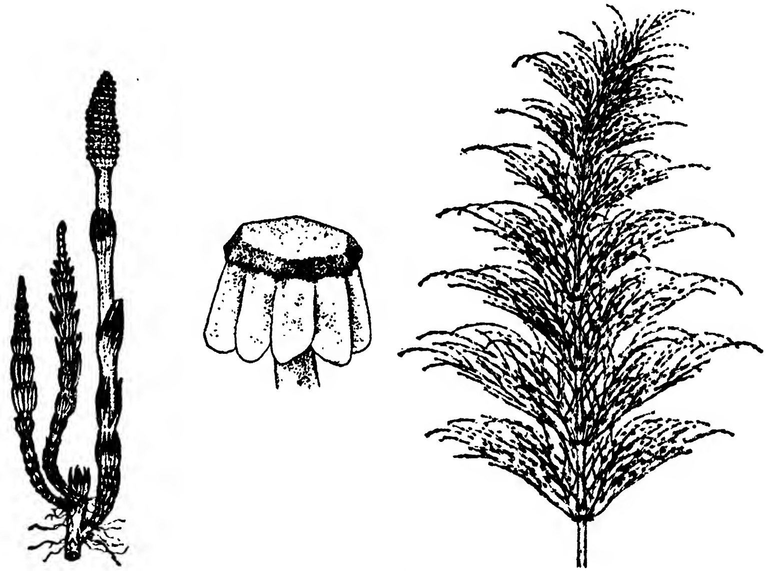


FIG. 859. *Equisetum arvense*

Left, sporophyte with fertile branch (at the right) and two young sterile branches (at the left) (× ½); center, shield-shaped sporophyll with old sporangia (× 10); right, sterile branch (× ⅓)

CLASS *EQUISETINEAE* (HORSETAILS)

Equisetum

General characteristics. During Carboniferous times the *Equisetineae* were a dominant element of the flora and included large tree forms. All the living *Equisetineae* are included in the single genus *Equisetum*, and are rather insignificant representatives of a once great race. As in all of the *Pteridophyta*, there is an alternation of a conspicuous sporophyte (Figs. 859, 860) and a small inconspicuous gametophyte (Fig. 864). The sporophytes of *Equisetum* are all comparatively small plants, the giant of the genus being a slender species, *Equisetum giganteum*, which has slender upright stems that reach a height of ten meters and have a diameter of only two or three centimeters. A sporophyte always has an underground rhizome from which hollow erect aerial branches arise. In some cases the aerial branches are unbranched and the sporophylls are borne at the tips in conelike aggregations called strobili (Fig. 860). In a very common species, *Equisetum arvense*, the upright aerial shoots are of two types (Fig. 859): unbranched shoots with terminal strobili, and much-branched vegetative shoots which serve for photosynthesis. A fancied resemblance of the much-branched structure to a horse's tail is responsible for the popular name horsetail. The stems consist of nodes and long, ribbed internodes. The outer part of the stem is usually heavily impregnated with silica; so much so, that the stems were formerly used as scouring material. This use gave rise to the

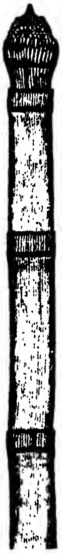


Fig. 860. Tip of a branch of *Equisetum hiemale* ending in a strobilus. (× 1)

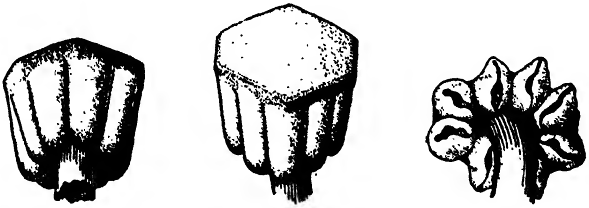


Fig. 861. Sporophylls of *Equisetum arvense*

Left, sporophyll with unopened sporangia as viewed somewhat from below. Center, same viewed somewhat from above. Right, umbrellalike top of sporophyll with open sporangia as seen from below. (× 10)

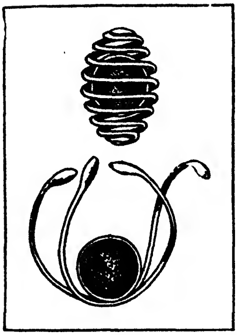


Fig. 862. Spores of *Equisetum arvense* showing different positions of elaters. (× 150)

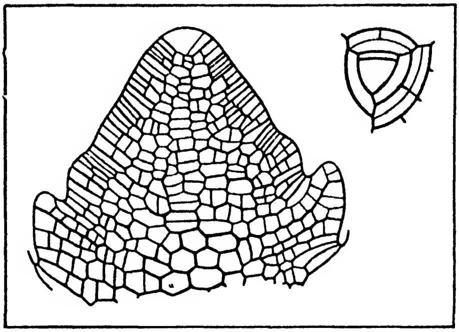


Fig. 863. Growing point of *Equisetum*

Left, longitudinal section through tip of a single apical cell, the divisions of which are responsible for increase in length. Right, cross section through apical cell. (After Goebel)

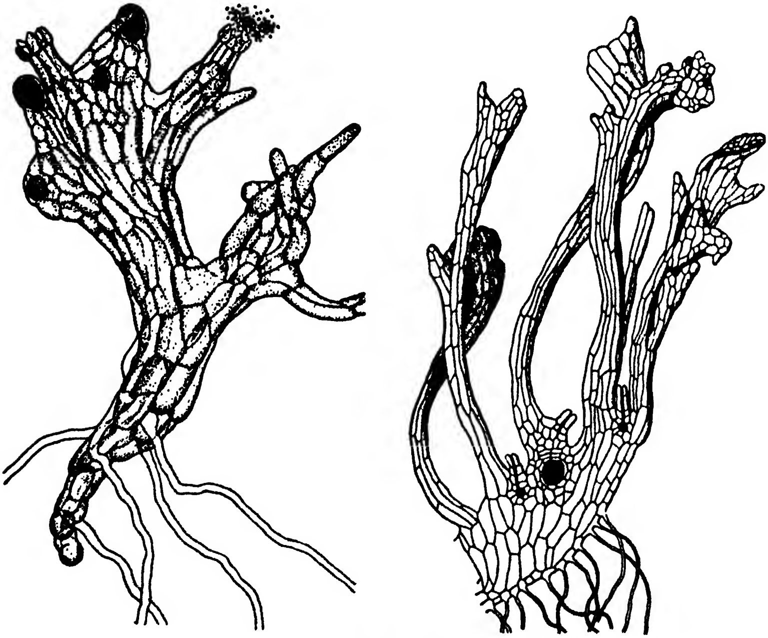


Fig. 864. Prothalli of *Equisetum*

Left, exterior view of male prothallus, showing antheridia, one of which is discharging spermatozoids (× 40). Right, section through female prothallus. The section is cut longitudinally through two archegonia and an embryo formed in a third archegonium. (× 45). After Thuret and Hofmeister

common name "scouring rushes." The leaves are small and scalelike, and are borne in whorls at the nodes.

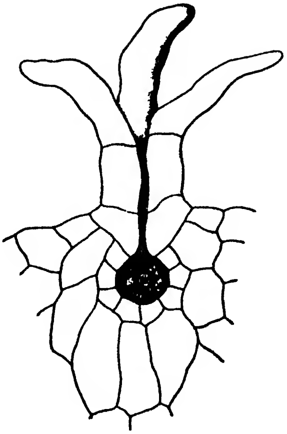


FIG. 865. Archegonium of *Equisetum arvense*. (× 350)

After Hofmeister

Sporophytes. The sporophores, or sporophylls, are highly characteristic. They have polygonal flat tops (Fig. 861). The stalk is attached to the center of the lower surface of this top. The sporangia are also attached to the lower surface, and form a circle around the stalk (Fig. 861). Attached to one point of the mature spore are four long, slender elaters (Fig. 862). These are formed by the spiral splitting of the outermost coat of the spore. This outer layer remains attached to the spore at the point where the elaters come together, thus fastening them to the spore.

Prothallus. The gametophyte produced by the spore is like that of the ferns in that it is a small green thallus. It is differently shaped from the usual fern prothallus, and much more branched (Fig. 864). *Equisetum* is usually dioecious. The archegonia are very like those of ferns (Fig. 865). The sporophyte begins to develop in the archegonium in much the same way as in ferns (Fig. 867), and, as in ferns, is soon an independent plant.

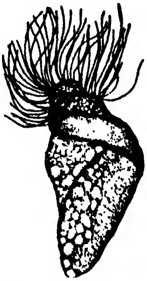


FIG. 866. Spermatozoid of *Equisetum*

After Sharp

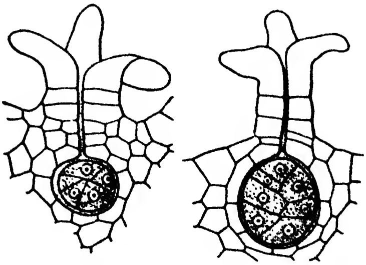


FIG. 867. Young embryos in archegonia of *Equisetum*. (× 215)

After Sadebeck

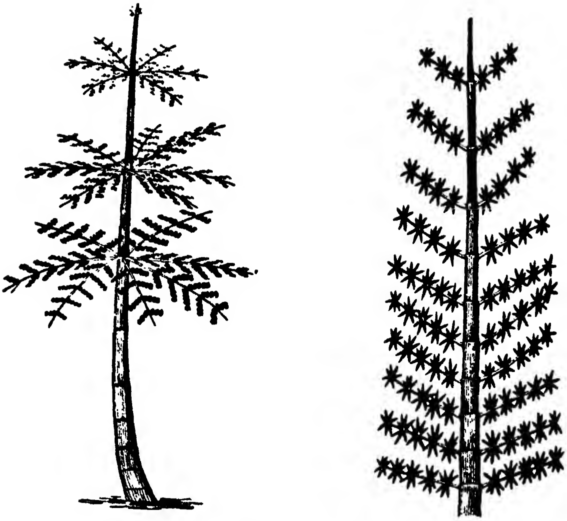


Fig. 868. *Neocalamites knowltoni*

Left, habit of plant; right, a branch, showing leaves in whorls. (× $\frac{1}{35}$)
After Berry

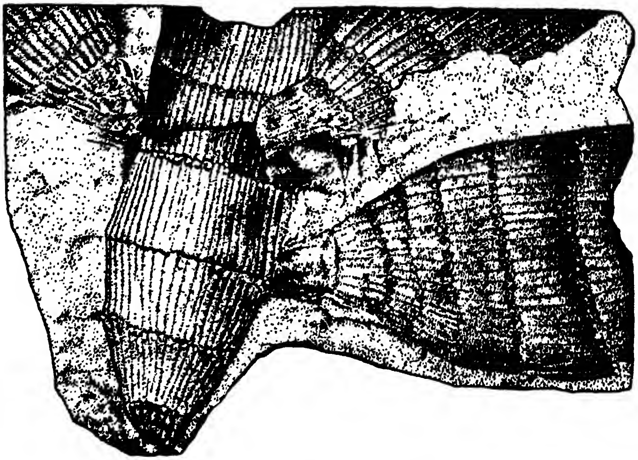


Fig. 869. *Calamites suckowi*

After Zeiller

Alternation of generations. The alternation of generations is like that of ferns. It consists of an alternation of a haploid gametophyte and a diploid sporophyte. The sporophyte ends with the spore mother cell, and the gametophyte starts with the spore.

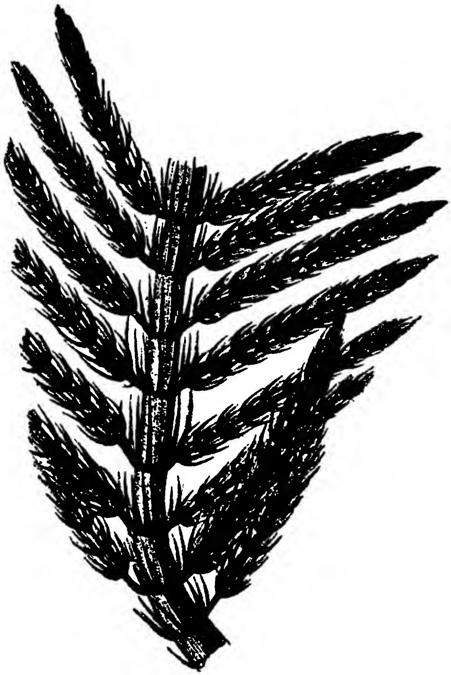


Fig. 870. Branch of calamite

After Grand' Eury

Fossil *Equisetineae*

Geological history. The *Equisetineae* made their first appearance as very primitive forms in the Devonian period. They reached their greatest development during Carboniferous times, and were represented by many tree forms (Fig. 1037). By the beginning of the Mesozoic they had declined greatly: they were represented by fair-sized plants (Figs. 868, 1032), but these were nothing like so large as the giants of the Carboniferous. They continued to decline, and soon were represented, as at present, by only comparatively small species.

During the Carboniferous, two extinct families of the *Equisetineae*, the *Calamitaceae* and the *Sphenophyllaceae*, were well

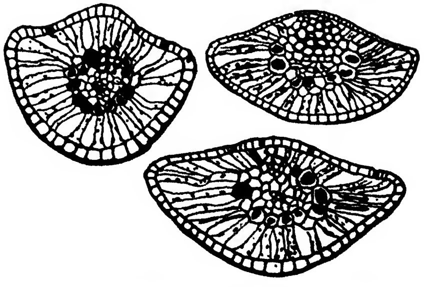


Fig. 871. Sections of calamite leaves

After Thomas

represented. The *Calamitaceae* included the giant forms, or calamites (Fig. 1029), while the *Sphenophyllaceae* consisted of weak, slender plants which are generally believed to have scrambled over other vegetation (Fig. 1029).

Calamitaceae. The general appearance of species of the family *Calamitaceae*, which is typified by the genus *Calamites*, was not unlike the modern genus *Equisetum* except that a great many of them reached tree size, perhaps a height of twenty or thirty meters. *Calamites*, like *Equisetum*, had prostrate rhizomes, most probably underground, from which the upright stems grew. The latter were huge hollow structures with branches and small leaves arranged in whorls.

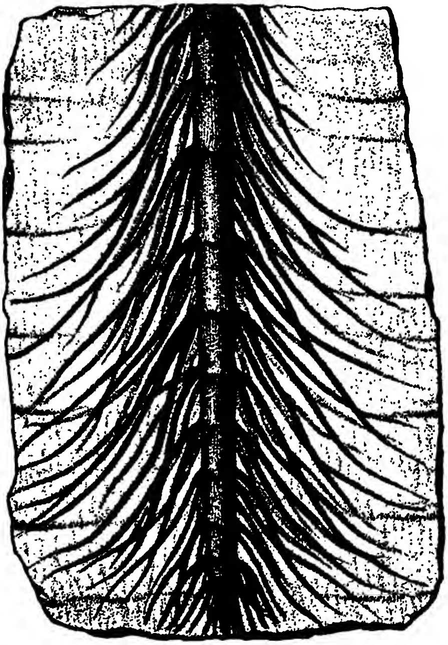


Fig. 872. Roots of a calamite

After Grand' Eury

The young stems were similar to *Equisetum* in structure, but they soon developed secondary thickening of a type very much like that seen in modern seed plants. The secondary wood, in some cases, reached a thickness of five centimeters, and the bark was even thicker.

The most numerous fossils are casts of the stem cavity (Fig. 869). These casts are marked by vertical ridges and furrows. The casts show distinct joints or nodes marked by zigzag furrows running across the longitudinal furrows. The cause of these markings is that the softer parts of the stem had decayed and the vascular bundles produced impressions in the form of furrows. The ridges correspond to the pith rays, which had disappeared before the cast was formed.

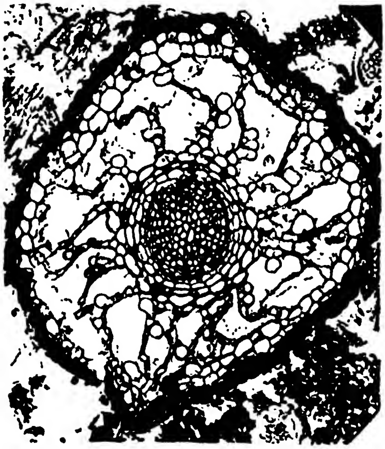


Fig. 873. Cross section of small root of a calamite

After Williamson and Scott

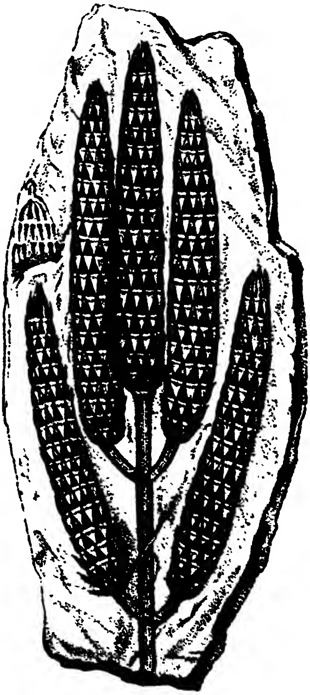


Fig. 874. Strobili of *Calamites*

The leaves of *Calamites* were like those of *Equisetum* in that they were arranged in whorls with the bases joined together (Figs. 870, 871).

The sporangia were borne in whorls in strobili, as in *Equisetum* (Figs. 874, 875). The sporophyll was like that of *Equisetum* in that it was umbrellalike with a shield-shaped top and with the sporangia on the under surface of the top. There were four sporangia on each sporophyll.

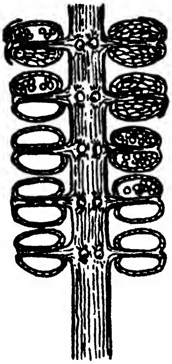


Fig. 875. Section through strobilus of a calamite in which the strobilus consisted entirely of sporophylls

After Renault

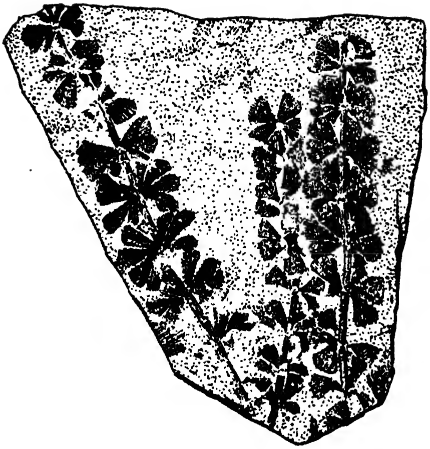


Fig. 876. *Sphenophyllum emarginatum*

After Zeiller

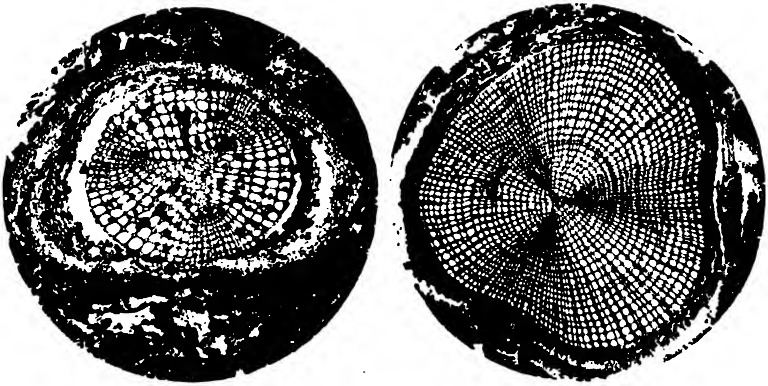


Fig. 877. *Sphenophyllum plurifoliatum*

Left, section of fairly young stem, but one with secondary thickening (× 13). Right, cross section of the xylem of a much older stem; note extensive development of secondary wood (× 6) After Williamson and Scott

In some cases the strobili bore only sporophylls (Fig. 875); in others there were also whorls of sterile leaves or bracts (Fig. 874). In different genera the sporophylls were attached in the axils of the bracts, midway between the whorls of bracts, or just below the bracts.

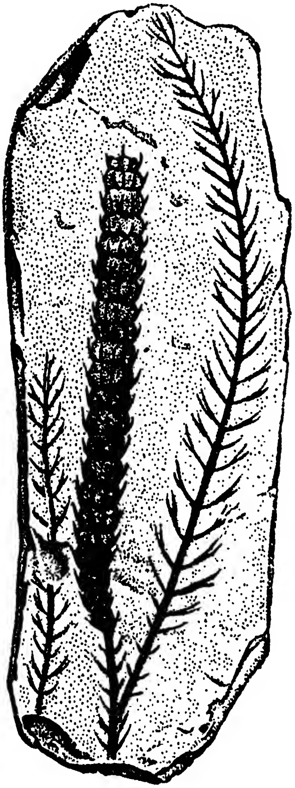


FIG. 878. Strobilus of *Sphenophyllum*

After Schimper

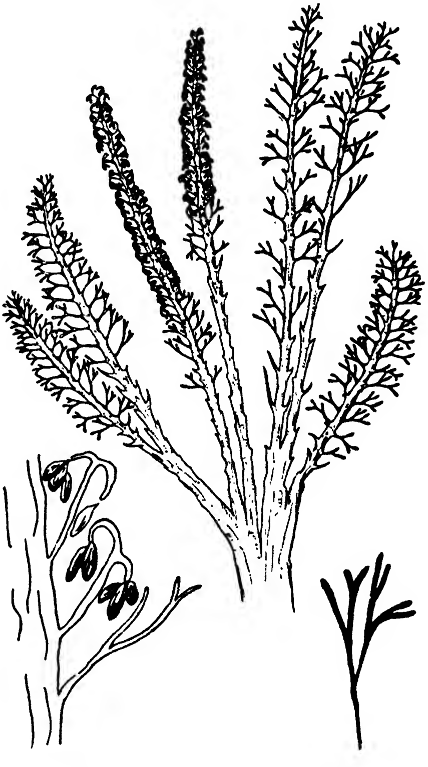


FIG. 879. *Hyenia elegans*, a primitive member of the *Equisetales*

Center, the plant with two fertile branches and five leafy branches. Lower left, sporophores with sporangia; lower right, sterile leaf. (After Krausel and Weyland)

In most species the spores were all of one size; but in a few cases some sporangia contained small spores (microspores) and others large spores (megaspores). Judging by analogy with living plants, it is believed that the megaspores gave rise to female prothalli and the microspores to male prothalli.

Sphenophyllaceae. The sphenophyllums had slender ribbed stems, about the size of a lead pencil or smaller (Figs. 876, 1029). The ribs did not alternate at the nodes as in *Equisetum*, but ran the entire length of the stem. The leaves were small and in whorls. Those of one whorl were directly above those of the next whorl and not alternate with them. The leaves at a node were in multiples of three; they were usually wedge-shaped, and the margins varied from entire to deeply dissected.

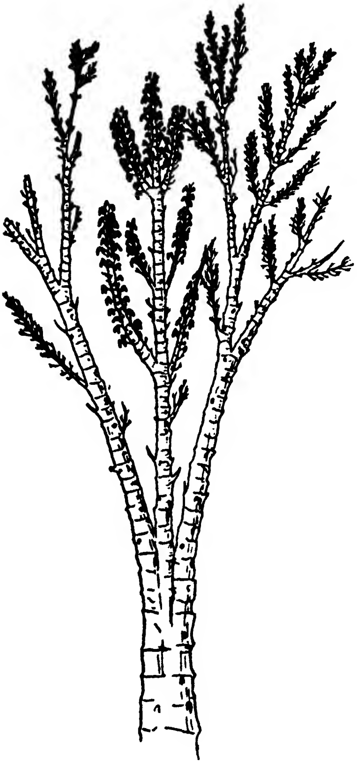


Fig. 880. ***Calamophyton primaevum*, a primitive member of the *Equisetales***

Note numerous sporangia on central branch. (After Krausel and Weyland)

The xylem of the stem was triangular, and, although the stems were slender, there was secondary thickening (Fig. 877). The sphenophyllums are usually regarded as having had aerial stems, which may have received support from scrambling over other plants. Some authorities believe that they were aquatics.

In most of the *Sphenophyllaceae* the sporangia were borne in strobili (Fig. 878), but the arrangement of the sporangia in the strobilus varied greatly in different species.

Relationship of *Equisetineae.* It seems clear that since Devonian times the *Equisetineae* have represented a distinct line of evolution, and that since Carboniferous times they have not developed along new lines. In their day the *Calamites* were dominant tree forms, but they lost out, and their place has been taken by seed plants.

As far as is known, the *Equisetineae* appeared after the *Psilophytales*. The earliest representatives were simple forms having points in common with the *Psilophytales,* and so it seems probable that they developed from a generalized stock which to us is represented by the *Psilophytales* that we know.

In the middle Devonian strata are found the most primitive and ancient known representatives of the *Equisetineae.* These are *Hyenia* (Fig. 879) and *Calamophyton* (Fig. 880). The stems of *Hyenia* were not jointed, but the forked leaves were in whorls. The fructification was a loose spike, the axis of which bore numerous spore-bearing organs or sporophores and no sterile bracts. It seems best to use the term sporophore rather than sporophyll, so as not to imply that these structures were leaves. The sporophores were forked, and each arm bore two or three sporangia. *Calamophyton* had jointed dichotomously branching stems. The leaves were forked and in whorls. The sporophores, as in *Hyenia,* were in loose spikes without sterile bracts. The sporophores were forked, with a single sporangium at the end of each arm of the fork. The dichotomous branching of the stems is a feature found generally in the *Psilophytales,* while the forked sporangiophores recall the dichotomously branched tips of the fertile branches of *Psilophyton.* However, these plants appear to be closely related to the *Equisetineae* and particularly to the *Sphenophyllaceae,* and thus seem to serve as a connecting link between the *Psilophytales* and the *Equisetales.*

Fig. 881. *Lycopodium reflexum,* with sporophylls scattered over the stem. (× ½)

CLASS *LYCOPODIINEAE* (CLUBMOSSES)

The *Lycopodiineae* are like the *Equisetineae* in that the living representatives are small plants and play a relatively unimportant part in our present flora, while other representatives were dominant plants in Carboniferous times and reached tree size. The two most important living genera are *Lycopodium* and *Selaginella.* The sporophyte is differentiated into stems, roots, and leaves. The leaves of living species are always small. The spermatozoids of these genera are biflagellate as in the *Bryophyta* and not multiflagellate as in ferns and *Equisetum.*

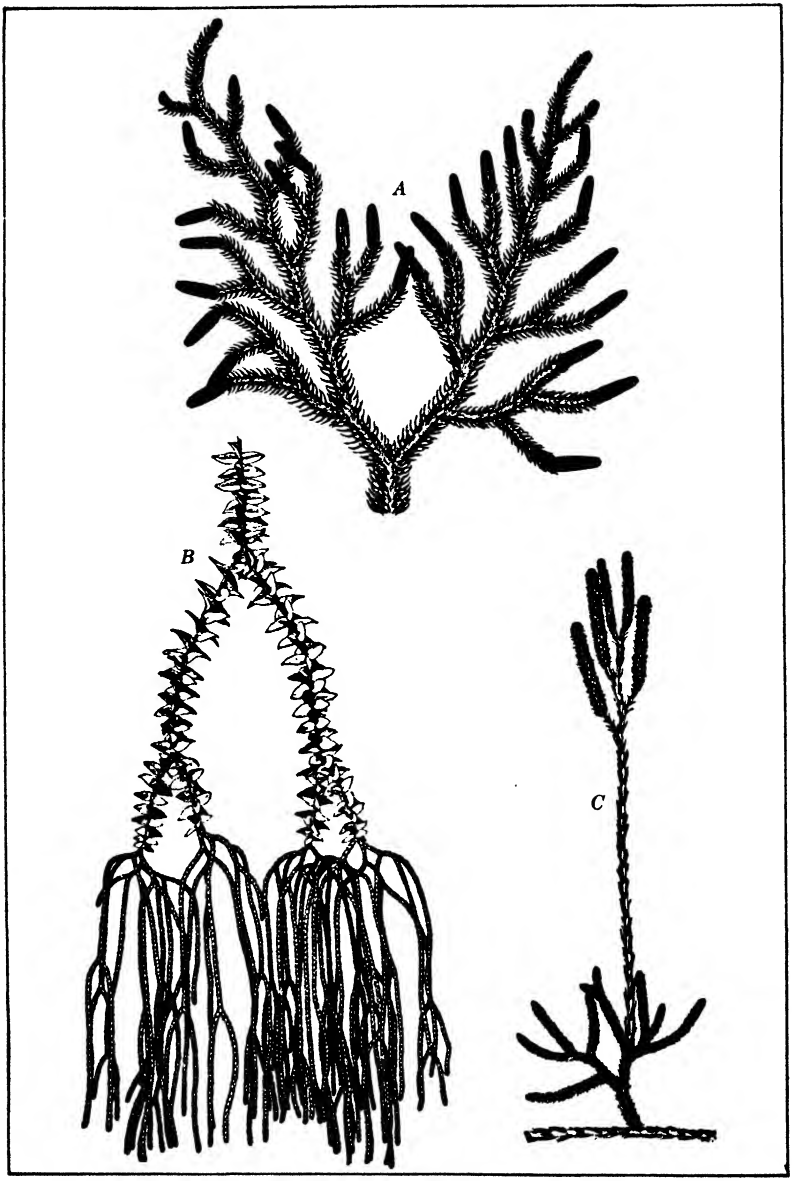


Fig. 882. Portions of sporophytes of *Lycopodium* with terminal strobili

A, a terrestrial tropical species (*Lycopodium cernuum*) (× ⅔); *B*, an epiphytic tropical species (*Lycopodium phlegmaria*) (× ¼); *C*, a terrestrial species (*Lycopodium clavatum*) found in the temperate zone and on tropical mountains (× ⅓)

Lycopodium

General characteristics. *Lycopodium* is a common and widely distributed genus of small or fairly small plants. In the temperate zone they are terrestrial and are known as ground pines (Figs. 881, 882). In the tropics there are both terrestrial and epiphytic species (Fig. 882).

As in other *Pteridophyta,* there is an alternation of a conspicuous sporophyte and a small inconspicuous gametophyte (Fig. 886). The stems in most species are much branched, with dichotomous branching. The stems are more or less thickly covered with small pointed leaves which are usually spirally arranged. Each has a single median vascular bundle. The sporangia are borne singly on the upper surface near the base of a leaf (Fig. 883). The sporophylls (leaves with sporangia) may resemble the ordinary leaves and be scattered over the stem (Fig. 881), or they may be somewhat different in shape and be aggregated in terminal strobili (Fig. 882).

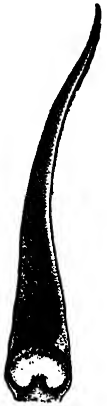


Fig. 883. A single sporophyll of *Lycopodium*, with sporangium on the upper surface near the base. (× 5)

The center of the stem is occupied by a conspicuous vascular bundle (Fig. 885). In this there are plates of tracheary tissues, or xylem, between which are masses of phloem. In erect species the xylem is usually arranged more or less radially. In structure the vascular bundle recalls that of *Asteroxylon.*

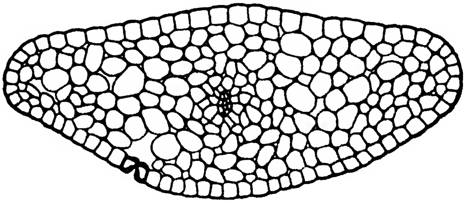


Fig. 884. Cross section of a leaf of *Lycopodium*. (× 105)

Gametophyte. The spores of *Lycopodium* germinate to produce a prothallus. This is a small structure which bears antheridia and archegonia. The character of the prothallus is quite different in different cases. In some forms it is a lobed, branched structure with chlorophyll, somewhat like the prothallus of *Equisetum*, although it is more tuberous than the latter (Fig. 886). In some temperate-zone forms it is a tuberous underground structure without chlorophyll and lives saprophytically with mycorrhiza (Figs. 887–890). The gametophytes bear numerous antheridia (Figs. 886, 888, 889, 891) and also archegonia which have the typical structure of a pteridophyte archegonium (Fig. 892). The spermatozoids are biflagellate (Fig. 891), in which respect they agree with the *Hepaticae* and differ from the ferns, where spermatozoids are multiflagellate. As in other pteridophytes, a spermatozoid swims to

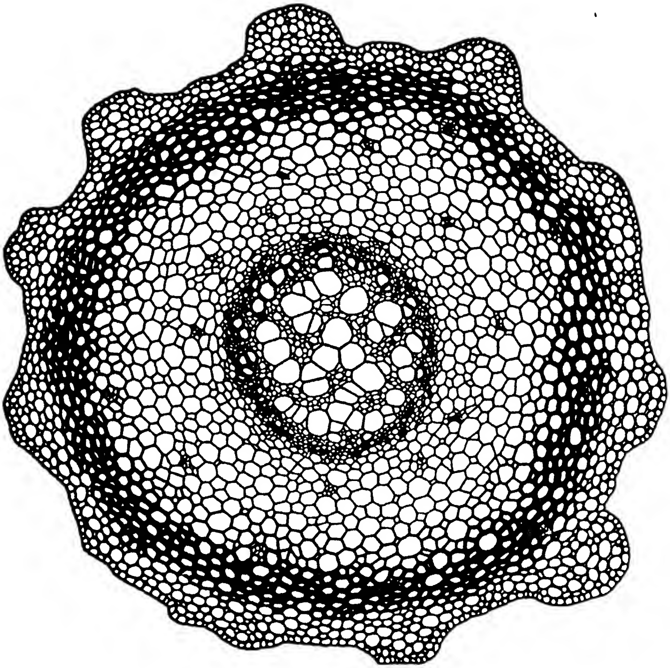


Fig. 885. Cross section of a stem of *Lycopodium cernuum*

Showing radial protostele in which phloem occurs between the strands of xylem. Note the sclerenchyma cells near the outer part of the cortex. (× 45)

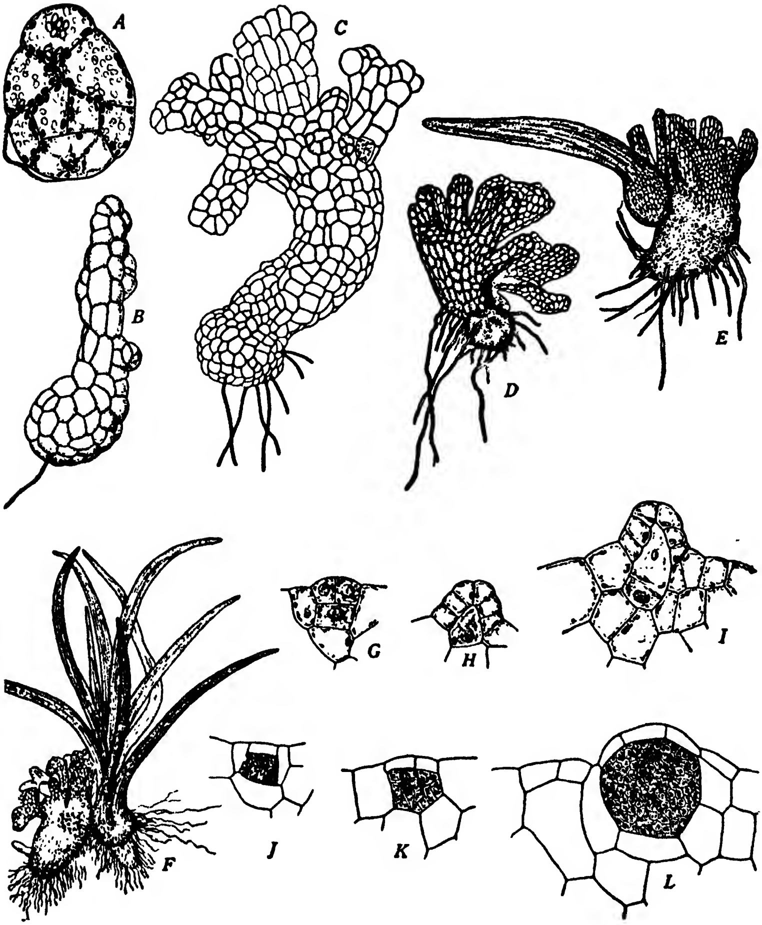


Fig. 886. Gametophyte of *Lycopodium cernuum*

A, early stage in formation of gametophyte from spore; note abundant chloroplasts in cells. *B*, later stage. *C*, still later stage; two archegonia and one antheridium are evident; the archegonia can be recognized by the four (shaded) neck cells; the antheridium is to the right of the archegonia. *D*, still older prothallus. *E*, prothallus with sporophyte attached to the left. *F*, gametophyte with older sporophyte. *G*–I, development of archegonium as seen in sections. *J*–*L*, development of antheridium as seen in sections. (*F*, × 1½; *G*–*L*, × 200). After Treub

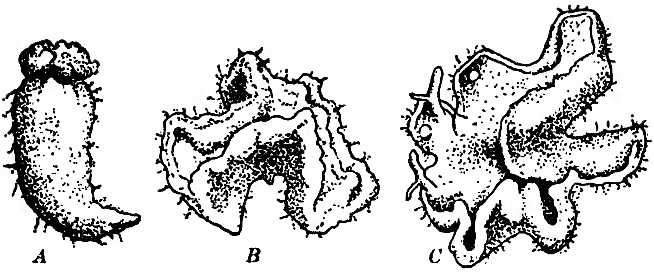


Fig. 887. Prothalli of temperate zone species of *Lycopodium*

A, *L. complanatum*; *B*, *L. clavatum*; *C*, *L. annotinum*. (After Bruchmann)

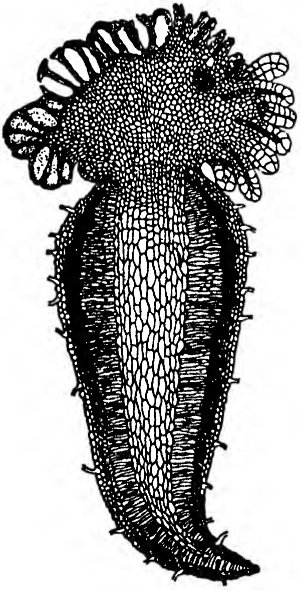


Fig. 888. Longitudinal section of prothallus of *Lycopodium complanatum*

To the left are numerous antheridia, some of which have discharged the spermatozoids. To the right are numerous archegonia; note embryo in one near the tip. (× 18). After Bruchmann

an archegonium and fertilizes the egg. Also, as in other *Pteridophyta*, the sporophyte is at first attached to the gametophyte by a foot and is dependent on the gametophyte (Figs. 889, 893). Again, as in other *Pteridophyta*, it soon becomes independent.

Alternation of generations. In *Lycopodium* the alternation of generations is like that of other *Pteridophyta* and consists of the alternation of a haploid gametophyte and a diploid sporophyte. The sporophyte begins with the fertilized egg and ends with the spore mother cells; the gametophyte begins with the spore.

Phylloglossum. There is one living genus of lycopods which is closely related to *Lycopodium*. This is *Phylloglossum*, an Australian genus with one species (Fig. 894). The mature plant consists of a tuberous stem with a few leaves and an elongated stalk terminating in a small strobilus. The tuberous stem with its leaves is rather similar to a juvenile stage in some species of *Lycopodium*. The gametophyte is also similar to those of some species of *Lycopodium* where the base of the prothallus

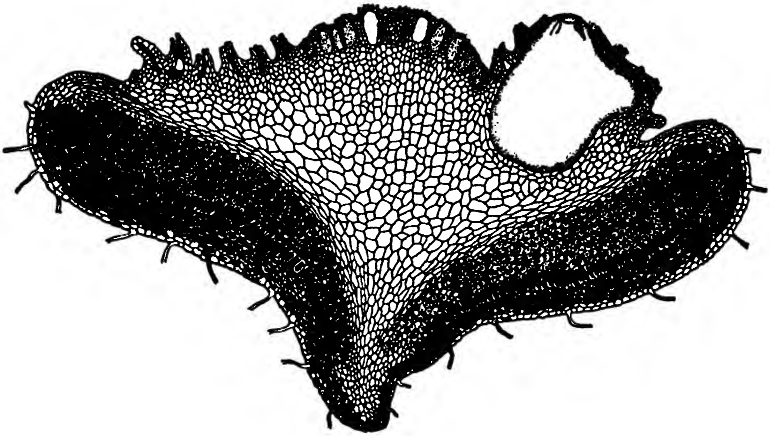


Fig. 889. ***Lycopodium*****. Longitudinal section through prothallus of** ***Lycopodium clavatum***

There are numerous antheridia in the center of the upper surface, and to the right and left of these are numerous archegonia. A young embryo is very evident to the right; note young shoot above, young root to the right, and large foot below and to the left. The mycorrhiza can be seen in the cells near the lower surface. (× 37). After Bruchmann

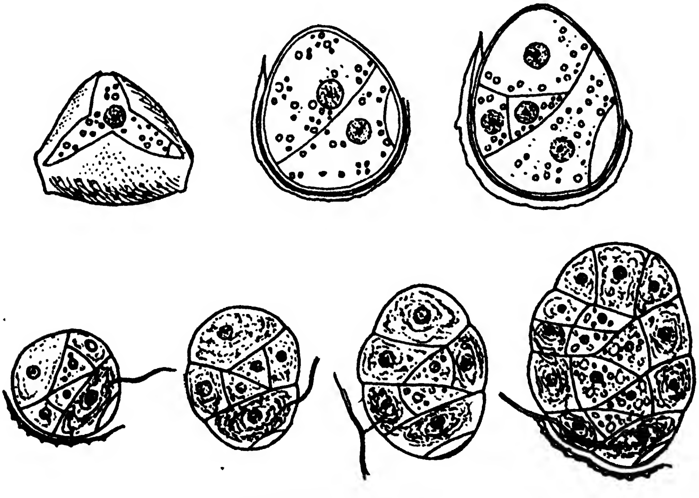


Fig. 890. ***Lycopodium***

Above, germination of spore of ***L. selago*** **(× 580). Below, entrance of mycorrhiza into very young gametophytes of** ***L. clavatum*** **(× 470). After Bruchmann**

is tuberous and there are green lobes on which the archegonia and antheridia are borne. In *Lycopodium* and *Phylloglossum* all the spores are alike. In the other two genera of living lycopods there are two kinds of spores, large spores which produce female prothalli and small spores which give rise to male prothalli.

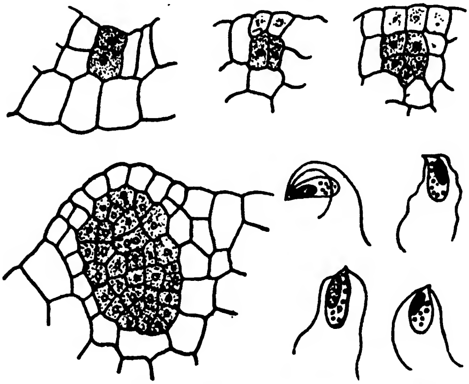


Fig. 891. Development of antheridia (× 150) and spermatozoids (× 550) of *Lycopodium clavatum*

After Bruchmann

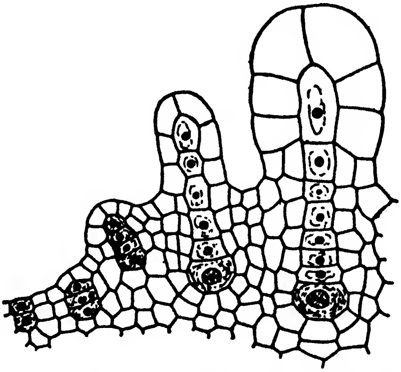


Fig. 892. Development of archegonium of *Lycopodium selago*

After Bruchmann

Origin of lycopods. The *Lycopodiales* with their small leaves seem to represent a different line of evolution from that seen in the ferns with their large leaves, and from that of the *Equisetineae* with their jointed stems. The anatomy of *Lycopodium* is very suggestive of that of *Asteroxylon* (Fig. 853), as are also the small, spirally arranged leaves. The *Psilotales* are in some respects intermediate between the *Psilophytales* and the *Lycopodiineae*. All the great groups of *Pteridophyta* had appeared before the end of the Devonian period, and the *Psilophytales* seem to represent a common and earlier Devonian stock from which the *Filicineae*, the *Equisetineae*, and the *Lycopodiineae* developed.

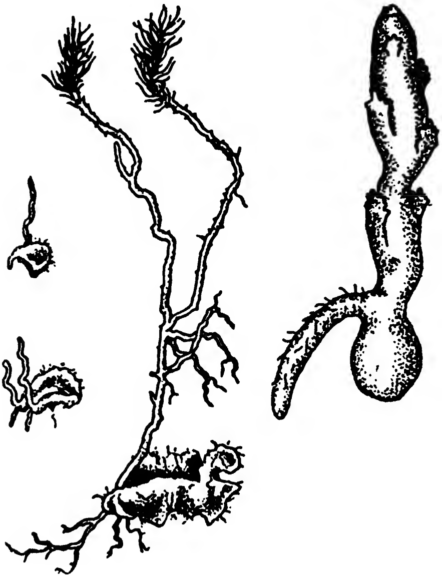


Fig. 893. ***Lycopodium clavatum***

Left, young sporophytes attached to prothallus; right, young sporophyte; below is the foot, to the left the root, and above, a shoot. (After Bruchmann)

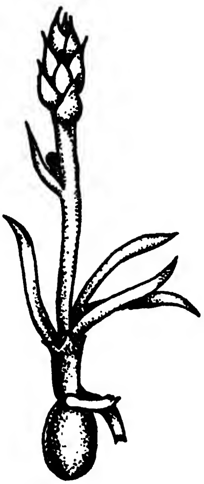


Fig. 894. ***Phylloglossum drummondii.*** **(× 3)**

After Bower

Selaginella

General characteristics. *Selaginella* is a large genus, with about five hundred or more species, of small or comparatively small plants. The sporophyte has branched stems with small leaves (Figs. 895–897). Some species of *Selaginella* grow upright and have

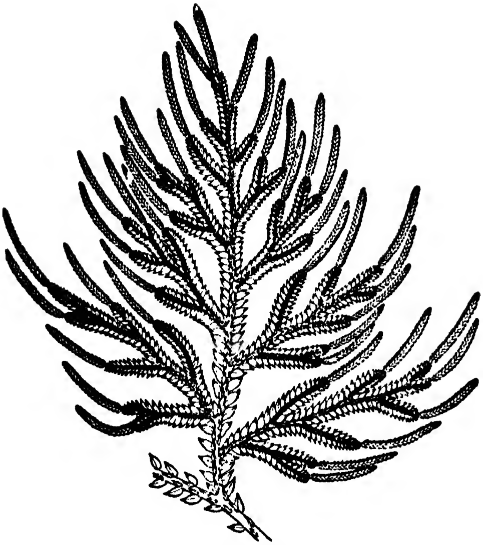


Fig. 895. Portion of a plant of *Selaginella* with sporophylls aggregated in terminal strobili

The entire upper branch is of limited growth. Note that it simulates the appearance of a fern frond. (× 1)

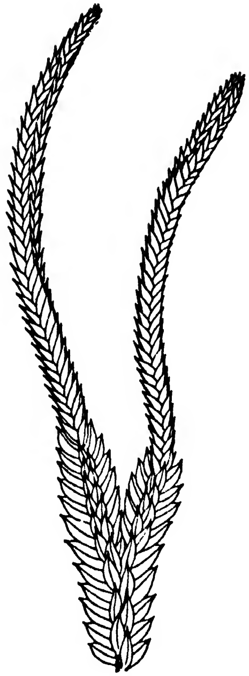


Fig. 896. Portion of a branch of *Selaginella* with two terminal strobili

Note the arrangement of the leaves in four rows. (× 2)

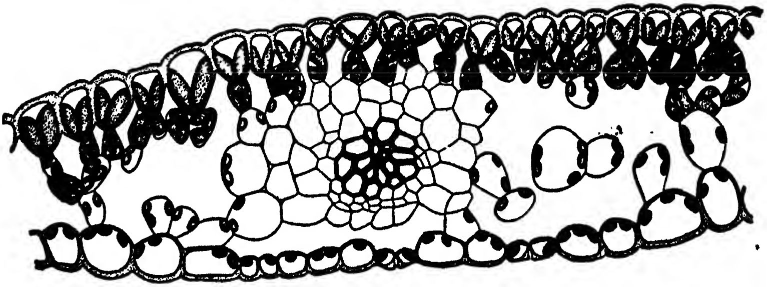


Fig. 897. Cross section of a portion of a *Selaginella* leaf. (× 235)

the leaves arranged radially around the stem. In most species the stems are more or less prostrate, and the leaves are in four rows (Fig. 896). In such cases the leaves of the two upper rows are much smaller than those of the two lower rows. Most of the species of *Selaginella* are tropical, particularly the showy ones, and some of these are cultivated for ornamental purposes. In many species there is a long creeping stem from which erect branches grow. Often a side branch produces a system of branches of limited growth which simulates the appearance of a fern frond (Fig. 895).

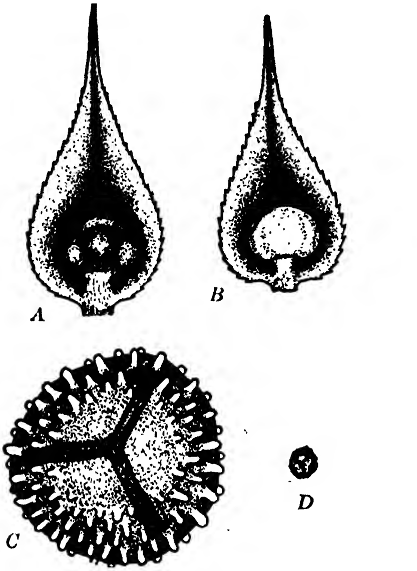


FIG. 898. Sporangia and spores of *Selaginella*

A, megasporophyll with megasporangium containing four megaspores (× 15); *B*, microsporophyll (× 15); *C*, megaspore (× 75); *D*, microspore (× 75)

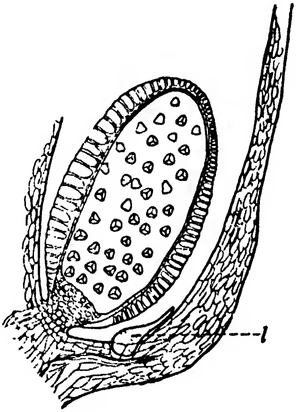


FIG. 899. Longitudinal section through microsporangium and base of microsporophyll of *Selaginella apus*

l, ligule. (After Lyon)

Ligule. Near the base of the leaf there projects from the upper surface a small appendage known as a ligule. This is said to absorb water. In sporophylls the ligule lies between the sporangium and the blade of the leaf (Fig. 899). Ligules are very characteristic of fossil lycopods.

Sporangia. The sporangia are borne singly on the upper surface near the base of sporophylls (Figs. 898, 899). In some species the sporophylls are similar to ordinary leaves, but in most cases they are smaller and are aggregated into terminal strobili (Figs. 895, 896, 900). The sporangia are of two kinds (Fig. 898), microsporangia and megasporangia, and the sporophylls which bear them are called respectively microsporophylls and megasporophylls. A microsporangium contains numerous small spores, microspores, while each megasporangium contains four large spores, megaspores. The microspores give rise to male prothalli, the megaspores to female prothalli.

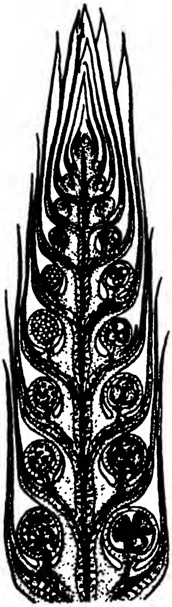


Fig. 900. Semi-diagrammatic longitudinal section of strobilus of *Selaginella*

Microsporangia represented on the left and megasporangia on the right. (After Sachs)

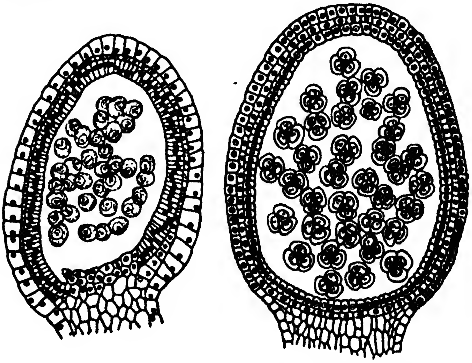


Fig. 901. Microsporangia of *Selaginella*

Left, microspore mother cells; right, microspores in tetrads. (After Lyon)

In their development the megasporangia give clear evidence of having been derived from the sporangia of some plant in which there was no differentiation into microsporangia and megasporangia. In the microsporangia a large number of spore mother cells are produced, and each of these divides to form four microspores (Fig. 901). In the megasporangia also a large number of cells which may be regarded as representing spore mother cells are produced (Fig. 902). All except one of these disintegrate, while the remaining one increases greatly in size and divides to produce four megaspores (Fig. 902). The only plausible explanation of the production of a large number of rudimentary mother cells in the megasporangium is that *Selaginella* is descended from a plant in which all these cells functioned as mother cells, and that by specialization it has come about that one mother cell grows at the expense of the others, which fail to develop. We may conclude that the heterosporous *Lycopodiineae* are descended from homosporous forms.

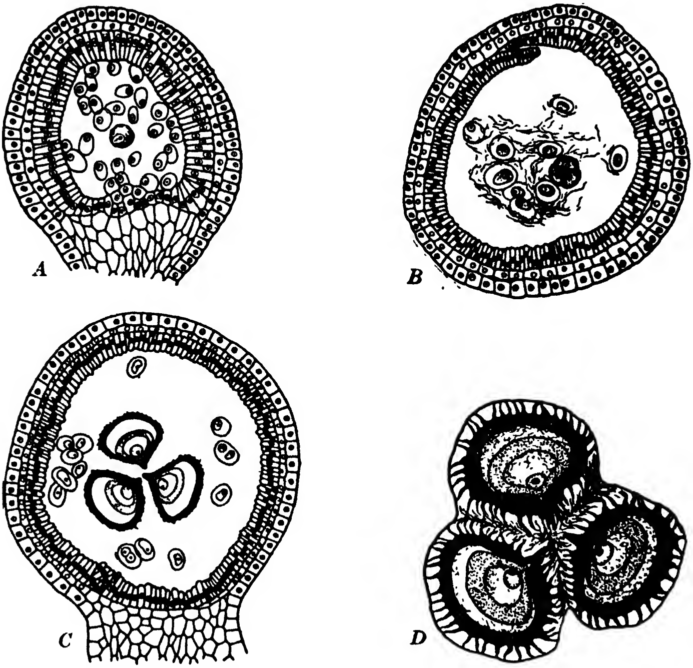


Fig. 902. Megasporangium and megaspores of *Selaginella*. (× 125)

A, longitudinal section of megasporangium with megaspore mother cell. The functional mother cell is much larger than the others. *B*, cross section of sporangium. The functional megaspore mother cell has divided to form a tetrad of megaspores. *C*, a functional tetrad has enlarged greatly. *D*, section of tetrad showing thick walls of spores. (After Lyon)

The male prothallus develops within the wall of a microspore, and consists of a single prothallial cell and an antheridium (Fig.

903). Since the whole gametophyte is formed within the spore wall, a vegetative prothallus is not necessary, and in the male gametophyte it is reduced to a single functionless cell. The antheridium has a sterile covering consisting of a single layer of cells, within which biflagellate spermatozoids are produced. The female prothallus likewise develops within its spore, the spore wall is burst, and the apex of the prothallus with the archegonia is exposed (Fig. 904). The egg is fertilized by a motile biflagellate spermatozoid, and the fertilized egg develops into a sporophyte (Figs. 905–906), as in other pteridophytes. In some cases archegonia may be produced, the eggs may be fertilized, and sporophytes may begin to develop, all before the spores are shed.

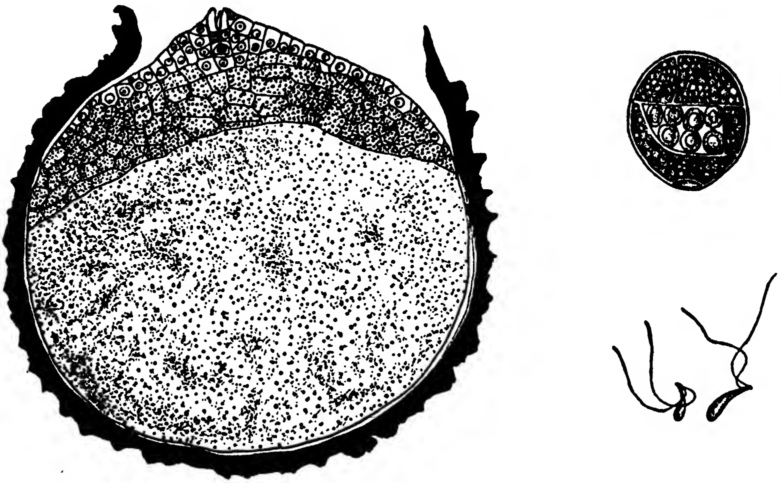


Fig. 903. Gametophytes of *Selaginella*

Left, section of a female prothallus; the megaspore wall is shown in black; note the archegonium projecting from the upper surface of the prothallus (redrawn after Miss Lyons). Upper right, male gametophyte of *Selaginella*; note that it consists of a single prothallial cell and a single antheridium (redrawn after Belajeff). Lower right, spermatozoids of *Selaginella* (redrawn after Belajeff)

Specialization of spores. The sporangia of *Selaginella* show greater specialization than do those of typical ferns in that they are differentiated into megasporangia and microsporangia. The differentiation of the sporangia and spores of *Selanginella* has been

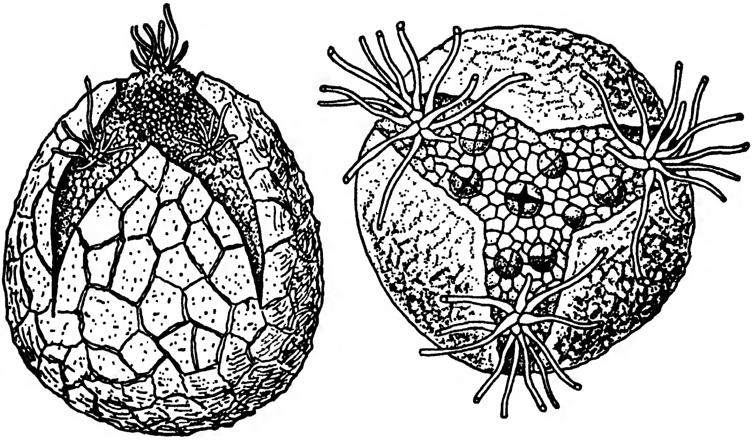


Fig. 904. Female gametophytes of *Selaginella*

Left, side view of *Selaginella kraussiana*. Note the manner in which the megaspore wall is cracked and opened by the growth of the prothallus. Three groups of rhizoids are very evident. The numerous archegonia can be distinguished by the four neck cells (× 50). Right, top view of *S. martensii*. The three groups of rhizoids are very prominent. In the prothallus are seen eight archegonia in various stages of development (× 125). After Bruchmann

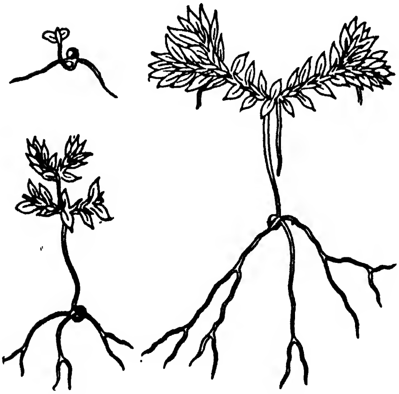


Fig. 905. Young sporophytes of *Selaginella kraussiana* still attached to megaspore. (× 1½)

After Bruchmann

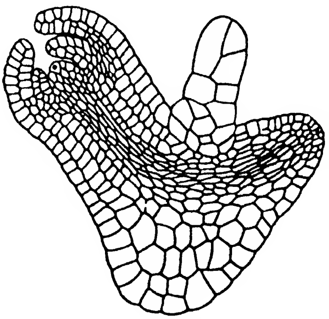


Fig. 906. Longitudinal section of young sporophyte

To the left and above is a young shoot. Note the apical cell. Above is the suspensor which serves to push the embryo down into the prothallus. To the right is a young root and below is the foot accompanied by a decrease in the size of the prothalli and a loss of their independence. They are small and are dependent for development on food stored by the parent sporophyte in the spore.

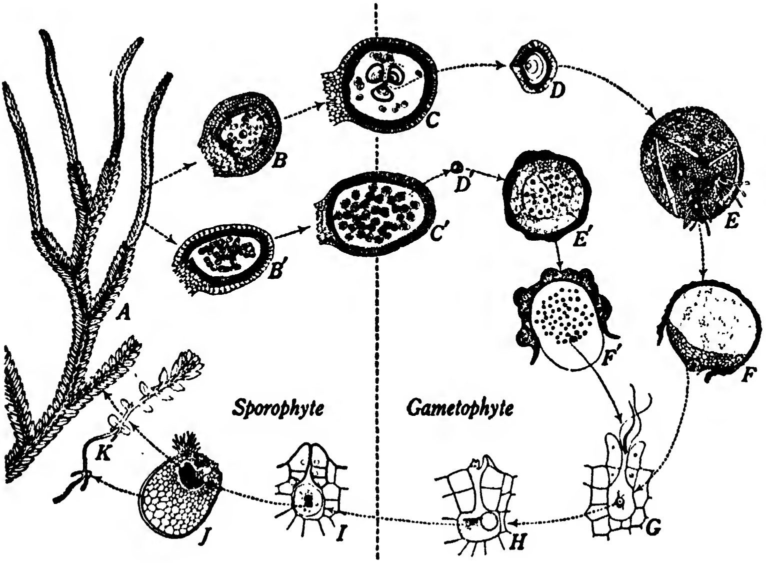


FIG. 907. Life cycle of *Selaginella*

A, portion of sporophyte with terminal strobili; *B*, megasporangium with megaspore mother cell; *B′*, microsporangium with microspore mother cells; *C*, megasporangium with tetrad of megaspores; *C′*, microsporangium with tetrads of microspores. The line separating the sporophytic and gametophytic generations is drawn through the sporangia because the sporangia themselves belong to the sporophytes while the spores represent the beginning of the gametophyte. *D*, section of megaspore; *D′*, microspore; *E*, female prothallus; *E′*, section of male prothallus; *F*, section of female prothallus with an archegonium; *F′*, section of mature male gametophyte with spermatozoids; *G*, spermatozoid entering an archegonium; *H*, spermatozoid ready to fuse with egg; *I*, fertilized egg, the beginning of the sporophyte; *J*, young sporophyte within gametophyte; *K*, old sporophyte still attached to gametophyte

The differentiation of spores into megaspores and microspores, and their dependence on the sporophyte, has certain obvious advantages. The delicate prothalli of ferns do not appear to be very well suited to life on dry land, as they require a considerable period of favorable moist conditions for their development. The

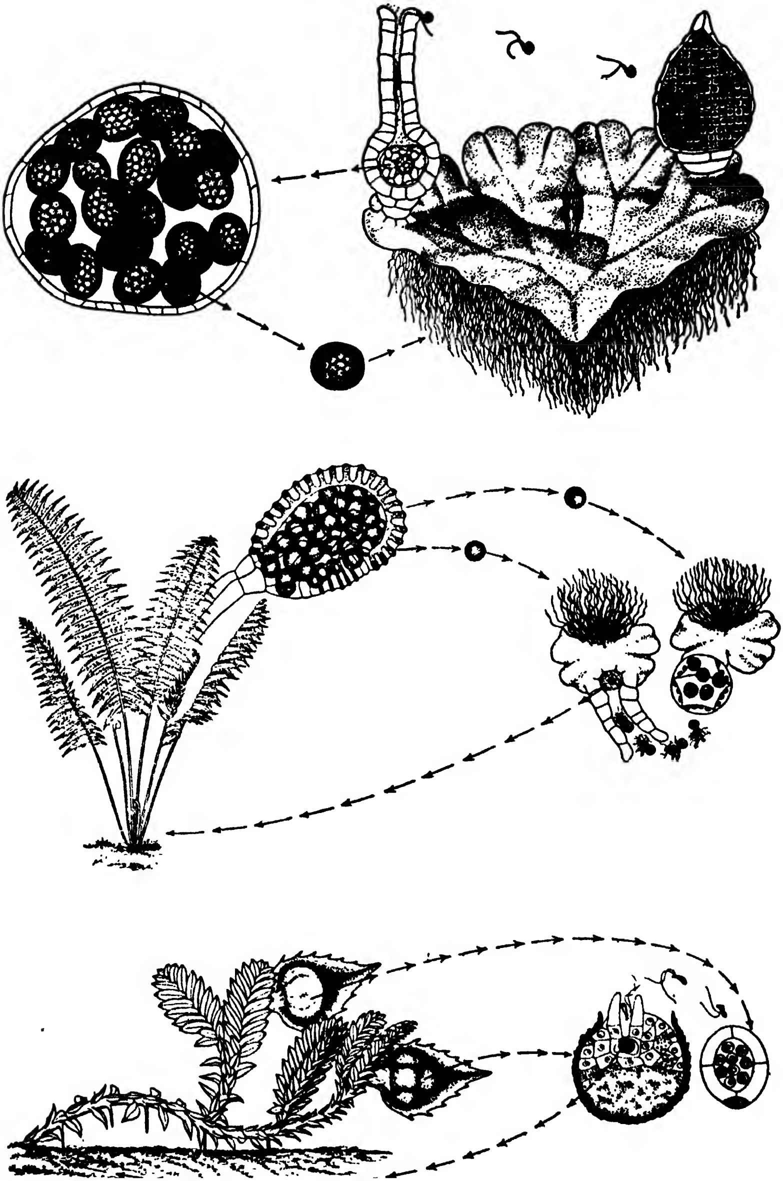


Fig. 908. Diagram showing relative development of sporophytes and gametophytes in *Bryophyta* and *Pteridophyta*

Above, *Riccia*; center, a fern; below, *Selaginella* sporophyte of a fern, on account of its structure, can withstand conditions that would be fatal to the prothallus. As the gametophytes of *Selaginella* derive their nourishment from the sporophyte, they are more independent of external conditions than are those of ferns.

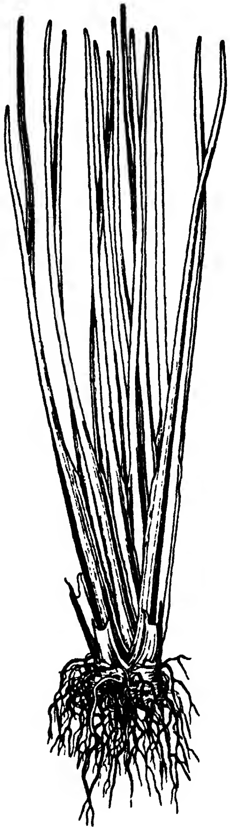


Fig. 909. *Isoetes.* (× ½)

Alternation of generations. In *Selaginella* there is, as in the other pteridophytes, an alternation of sporophytic and gametophytic generations (Fig. 907). The chief differences are that in *Selaginella* the sporophyte bears two distinct kinds of sporangia which form two different types of spores, megaspores and microspores; and that the megaspores produce female gametophytes, while the microspores give rise to male gametophytes. The spermatozoid from the male gametophyte fertilizes an egg in an archegonium of the female gametophyte, and, as in other *Pteridophyta*, the fertilized egg produces a sporophyte. In *Selaginella* the prominence of the sporophyte as compared with the gametophyte is relatively greater than in the ferns we have considered and in *Lycopodium*, in that both male and female gametophytes are greatly reduced in size and are dependent for nourishment on food stored by the sporophyte.

It is of interest to compare the gametophytes and sporophytes of liverworts, ferns, and *Selaginella* (Fig. 908). In all but the most advanced types of liverworts the sporophyte is entirely dependent on the gametophyte for nourishment. Even in *Anthoceros* the sporophyte is partially dependent on the gametophyte. In typical ferns the gametophyte and sporophyte are both independent plants. In *Selaginella* the gametophyte is greatly reduced in size and is dependent on the sporophyte for nourishment, the reverse of the condition in liverworts.

Isoetes. In addition to *Selaginella*, *Isoetes* is the only genus of living heterosporous pteridophytes which is included in, or even closely related to, the lycopods. The genus *Isoetes* is represented by a number of species, and is widely distributed. In general appearance the sporophyte resembles a tuft of grass (Fig. 909). The stem is very short and unbranched, and bears a large number of crowded, grasslike leaves. Each leaf is a sporophyll and has a single sporangium embedded in its enlarged base. The leaf resembles that of *Selaginella* in having a ligule. In *Isoetes* this is inserted above the sporangium (Fig. 910). A microsporangium contains very numerous microspores. A megasporangium (Fig. 910) likewise contains many megaspores, but nothing like so many as there are microspores in a microsporangium. In both microsporangia and megasporangia there are, in addition to the spores, plates of sterile tissue. The gametophytes are very similar to those of *Selaginella*. Each

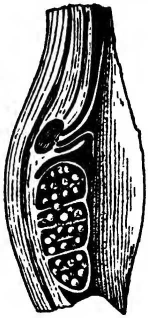


Fig. 910. Base of sporophyll of Isoetes with megasporangium

After Brongniart

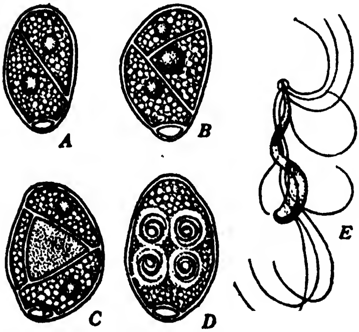


Fig. 911. Male gametophyte and spermatozoid of *Isoetes*

A, very young gametophyte (below, a single prothallial cell, and, above this, cells which will form the antheridium); *B*, *C*, further development of antheridium; *D*, antheridium with spermatozoids; *E*, spermatozoid. (After Belajeff)

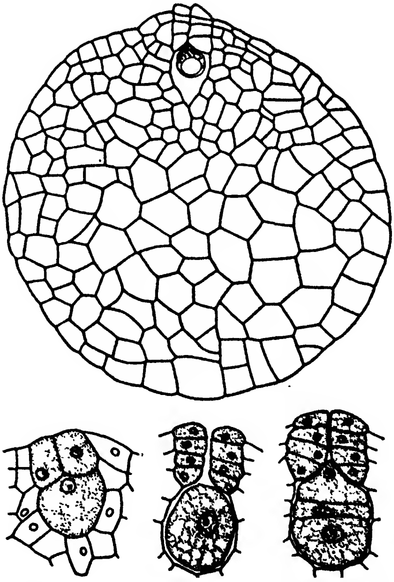


Fig. 912. Female gametophyte of *Isoetes* and development of archegonium

After Campbell and La Motte

microspore gives rise to a male plant which develops within the spore. The male plant consists of a single prothallial cell and an antheridium (Fig. 911). The female prothallus is developed within the megaspore and produces archegonia (Fig. 912). As in other *Pteridophyta*, the fertilized egg develops into a sporophyte.

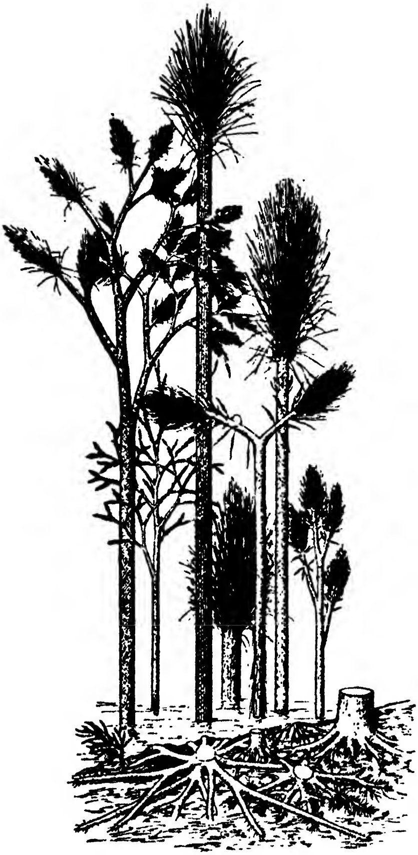


FIG. 913. ***Lepidodendron*, two figures to the left; and *Sigillaria*, five figures to the right**

After Grand' Eury

Isoetes is often included in the *Lycopodiineae*, but is sometimes placed in a class by itself. It differs from other lycopods in that it has multiflagellate spermatozoids, in which respect it resembles the *Filicineae* and *Equisetineae* rather than the *Lycopodiineae*.

Fossil Lycopods

General characteristics. In the Carboniferous period lycopods were very numerous, and ranged from small herbaceous species very similar to modern selaginellas to giant trees with extensively developed secondary thickening (Fig. 913). There may have been, and probably were, forms with only one kind of spore, as in *Lycopodium*; but certainly the great majority had megasporangia with megaspores and microsporangia with microspores, as in *Selaginella* (Fig. 914). The megaspores produced female prothalli with archegonia as in *Selaginella* (Figs. 915, 916), and so it may be supposed that the microspores gave rise to male prothalli. Evidently, as in modern forms, there was an alternation of a dominant sporophytic

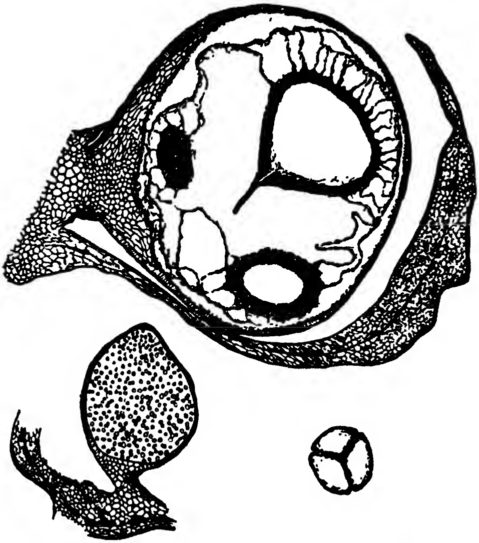


Fig. 914. Sporangia and spores of *Bothrodendron*, a Carboniferous lycopod

Above, section of megasporangium with megaspores; lower left, microsporangium; lower right, tetrad of microspores. (After Reed.) This *Bothrodendron* was like *Selaginella* in having a megasporangium with four megaspores. Another *Bothrodendron* had a number of tetrads of megaspores in the megasporangium. *Lepidodendron*, like *Isoetes*, had a large number of tetrads in each megasporangium

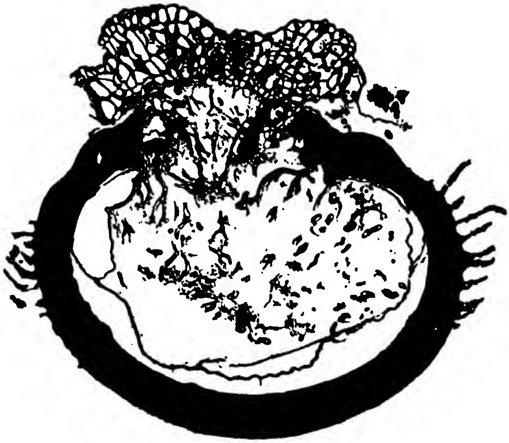


Fig. 915. Female prothallus of *Bothrodendron*

Note heavy megaspore wall; also partial sections of archegonium generation and a generation of small gametophytes. With the passing of the Paleozoic era the giant lycopods disappeared. It seems that these left no descendants, as the small lycopods of today appear to be relatives rather than descendants of the giants of the past.

The two most prominent genera of Carboniferous lycopods were *Lepidodendron* and *Sigillaria*, and only these two will be described.

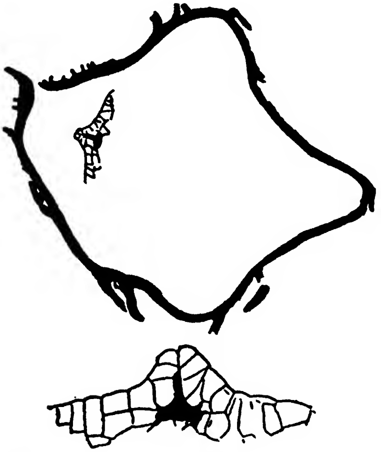


Fig. 916. Megaspore of *Lepidodendron veltheimianum*

Above, megaspore with portion of prothallus containing archegonium (× 50). Below, section of archegonium (× 140). After Gordon

Lepidodendron. This genus included numerous large trees (Figs. 913, 1029). One specimen more than thirty meters in height has been measured. The leaves were linear and arranged in spirals on the stem (Fig. 917), so that the leaf scars show a spiral arrangement (Figs. 917, 918). Like those of modern lycopods, the leaves were small for the size of the plants; but they were larger than those of the recent forms. The large trees were characterized by having single, tall trunks. The branching was dichotomous, and considerable branching resulted in a rather dense crown (Fig. 1029). The sporangia were in strobili at the ends of branches as in *Selaginella* and most species of *Lycopodium*. The strobili were formed of sporophylls, each with a single sporangium on its upper surface as in modern *Lycopodiales*. *Lepidodendron* was heterosporous.

The stem contained a single stele, which was not broken up into bundles as in the higher plants. In some cases the xylem formed a continuous ring around a central pith; in others, the xylem was solid. These different conditions were found not only in different species but even in the same individual, the ring of xylem being characteristic of the large stems of most forms. The majority show a considerable development of secondary tissues due to cambial activity between the xylem and phloem.

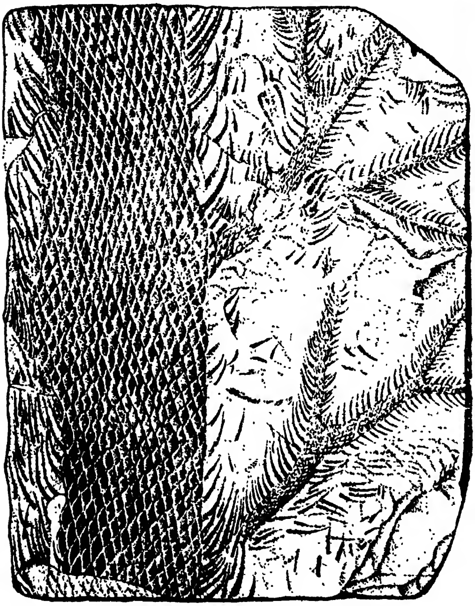


FIG. 917. *Lepidodendron lycopodioides*

Note small leaves and leaf scars. (After Zeiller)

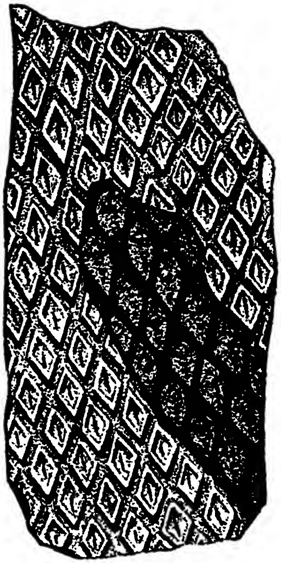


FIG. 918. Bark of *Lepidodendron diplotegioides*

An outer layer has been removed from a large part of the specimen. (After Schimper)

Sigillaria. This genus also contained large trees, thirty meters or more in height. They were often unbranched (Figs. 913, 1029), or sometimes the stem was sparingly divided dichotomously, forming a few large branches (Figs. 913, 1029). The leaves were long, reaching a length of a meter or more, and were often in terminal clusters. The leaf scars were usually in vertical rows; sometimes on elevated ridges (Fig. 919).

Sigillarias must have been rather bizarre in appearance. Some were tall and slender, while others were very large at the base and tapered rapidly.

The primary wood was in the form of a ring as in *Lepidodendron*, but differed from that of the latter genus in being broken up into separate bundles. The stem, like that of *Lepidodendron*, shows secondary thickening.

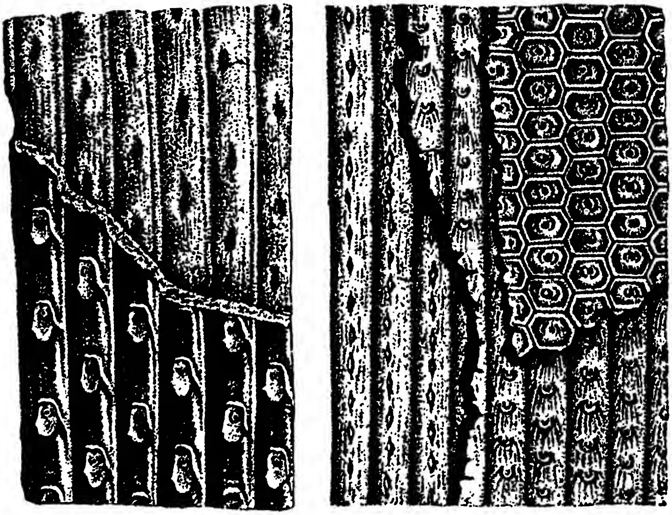


Fig. 919. Bark of *Sigillaria pachyderma* and *S. tessellata*

Note variation in appearance as layers are removed. (After Schimper)

The sporophylls of *Sigillaria* were in strobili resembling those of *Lepidodendron*. However, they were not borne at the ends of branches but in whorls or in vertical rows on the large stems. Some of the sigillarian strobili were very large, reaching a length of thirty centimeters and a diameter of six centimeters. It is believed that the strobili were generally heterosporous; that is, that they contained both megaspores and microspores.

"Seed." In some cases among the Carboniferous lycopods ,the differentiation of megasporangium and megaspore went so far as to produce seedlike structures (Fig. 920). This occurred in both herbaceous and arborescent forms. In such cases only a single megaspore developed, and this practically filled up the megasporangium.

This megaspore produced a prothallus which was permanently retained within the sporangium. Also, a sterile envelope, similar to an integument, grew up around the sporangium.

No embryos have been found within these "seed," but the absence of an embryo seems to be characteristic of Paleozoic seed. Functionally, the structures just described were seed. It is usually said that they differed from true seed in that they had no vascular system other than that of the bract or sporophyll; also that they were not detached independently, as were true seed of the Paleozoic era, but were shed attached to the bract or sporophyll, which served as a wing for the dispersal of the "seed" by the wind.

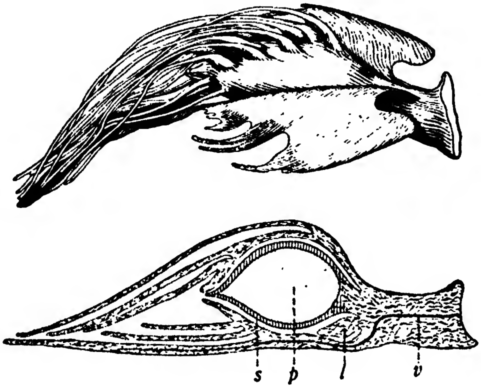


FIG. 920. "Seed" of *Miadesmia membranacea*

Above, sporophyll with "seed." Note long hairlike appendages on "seed." Below, section of sporophyll and "seed"; *s*, sporangium wall; *p*, prothallus; *l*, ligule; *v*, vascular bundle of sporophyll. Note that the sporophyll forms a covering around the sporangium. (After Benson)

The "seed"-bearing lycopods did not survive the Paleozoic era, and did not give rise to any of the modern seed plants.

CLASS *FILICINEAE*

General characteristics. Among all the *Pteridophyta* the *Filicineae* or ferns are characterized by having sporophytes with large leaves. In shape the leaves vary very greatly, ranging from very simple to very much compounded (Fig. 821). Some ferns are so small as to be mosslike, while others are trees (Fig. 821) reaching a height of eight or ten meters or more. In many the stem takes the form of a rhizome. While some ferns can live in rather dry situations, most of them are found in moist places. In warm and moist parts of the world, ferns are very numerous as epiphytes. The structure of ferns is much more varied than that of either of the other classes of living *Pteridophyta.* The ferns also far outrank the other classes of *Pteridophyta* both in number of species and in number of individuals.

Past history. At one time it was thought that ferns were exceedingly common during Carboniferous times; but it has been found that most of the fernlike fronds of the Carboniferous period bore seeds and so were seed plants rather than ferns. Plants which appear to be true ferns are known from the Devonian and also from the Carboniferous, but it would appear that the part played by the ferns in the flora of these ancient times was insignificant as compared with that of *Equisetineae* and *Lycopodiineae.* The plants of the mid-Devonian, as we have noted, were predominantly leafless. Most of the ancient ferns seem to have lacked laminae. The fronds were branched naked rachises on which the sporangia were borne terminally (Fig. 921). These original ferns were certainly very different from those of today.

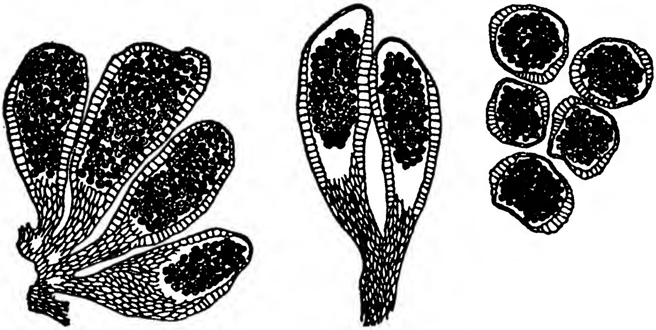


FIG. 921. Sporangia of *Zygopteris*

After Renault

Since the discovery that most of the ancient fernlike leaves with laminae belonged to seed plants, it has become more or less a question whether the remaining ones are ferns or seed plants. There are, however, some widely distributed forms with laminae (Fig. 922) in late Devonian and Carboniferous times which appear to be ferns. Large tree forms of a group which was abundant in the late Carboniferous and Permian, and practically confined to those times, have been regarded as tree ferns (Fig. 1029); although it has been suggested recently that they may be seed-ferns. They reached heights of about twenty meters, and were equal in stature to the tallest of living tree ferns.

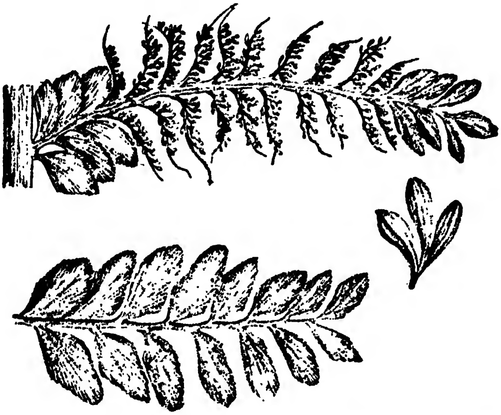


FIG. 922. *Archaeopteris hibernica*, a plant which is generally regarded as a fern Above, fertile leaf; below, sterile leaf; to the right, sporangia. (After Renault)

The sporangia of these ancient tree forms were not separate as in most modern ferns, but were united in groups, forming rings or rows, as in what is now a small family (*Marattiaceae*, Fig. 925) of tropical ferns, none of which are tree ferns. The ancient tree forms, if ferns, were much more closely related to the *Marattiaceae* than to modern tree ferns.

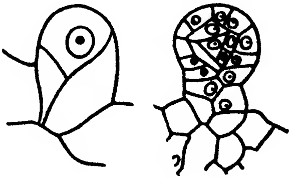


FIG. 923. Two stages in the development of the sporangium of *Dennstaedia punctilobula*, a leptosporangiate fern After Conard

Probably the ferns and seed-ferns are descended from a common stock, but they seem to have separated before either branch acquired lamina, as the earliest known seed-fern is without lamina (Fig. 952).

Ferns were very much more abundant during the Mesozoic than in the Paleozoic, and their abundance and importance seem to have increased up to the present day. As they have increased in abundance they have also undergone evolution, and most of the living ferns are of modern types.

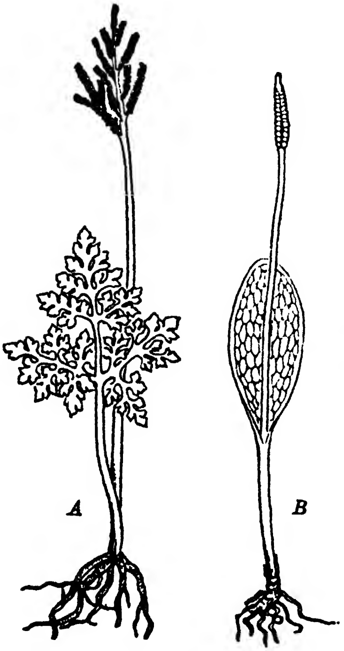


Fig. 924. The moonwort and adder's-tongue

A, the moonwort (*Botrychium ternatum*); *B*, the adder's-tongue (*Ophioglossum vulgatum*)

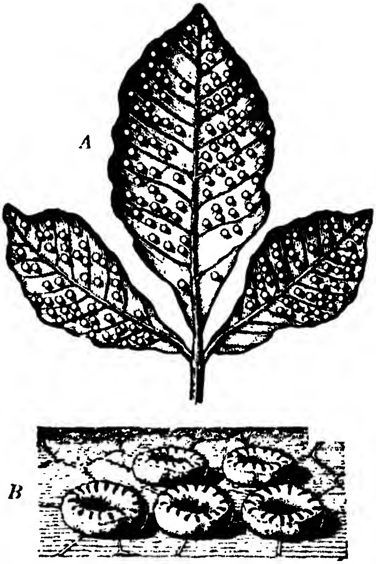


Fig. 925. *Christensenia cumingiana*, one of the *Marattiaceae*

A, a leaf with synangia (× $\frac{1}{3}$). *B*, enlarged view of synangia. Note openings in the individual sporangia

Eusporangiate and leptosporangiate ferns. The ferns are divided into two groups, the *eusporangiate* ferns and the *leptosporangiate* ferns. In the *Bryophyta* and also in the *Equisetineae* and *Lycopodiineae*, the sporogenous tissue develops from cells beneath the epidermis. This appears to have been true also of the *Psilophytales*, and is regarded as a primitive condition. Ferns in which sporogenous tissue is developed in this way are called euspo-

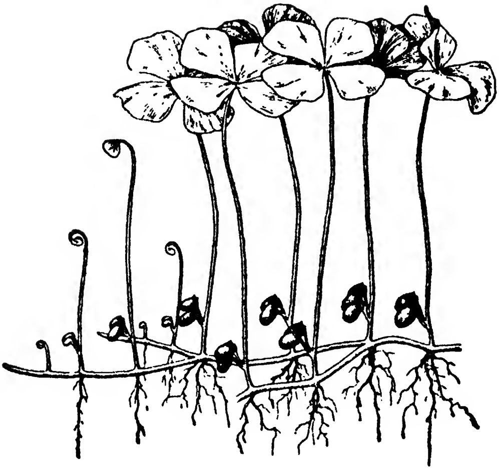


FIG. 926. *Marsilea*

Note cloverlike leaves and sporocarps attached to lower part of the stalks of the leaves

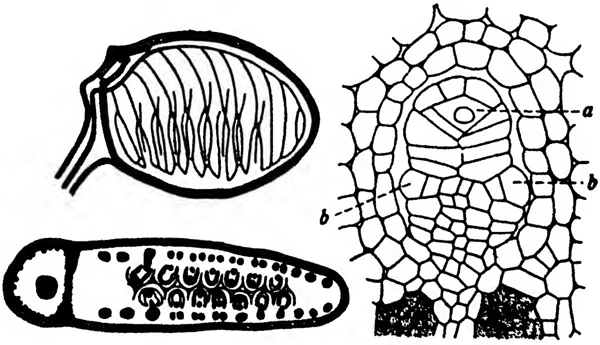


FIG. 927. *Marsilea* sporocarp

Upper left, inside of one valve showing veins going to the sori; lower left, section through sporocarp showing early stage in development of two rows of sori; right, longitudinal section of a single sorus. *a*, young megasporangium; *b*, *b*, cells which will give rise to microsporangia. (After Johnson) rangiate ferns. The eusporangiate ferns are regarded as more primitive than leptosporangiate ones.

In the typical leptosporangiate ferns the sporangium and its stalk are formed from an epidermal cell. Oblique walls develop in this cell in such a way as to form an apical cell, divisions of which result in the production of a sporangium (Fig. 923). While the typical eusporangiate and leptosporangiate sporangia are very distinct, gradations from one to the other occur in the simplest of the leptosporangiate forms.

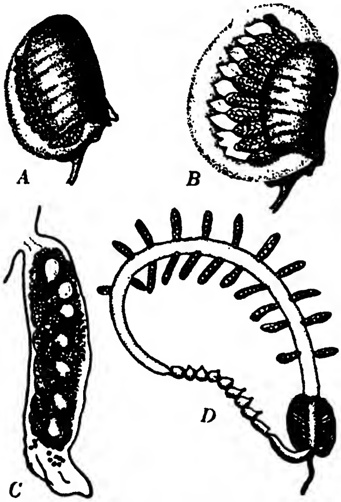


FIG. 928. *Marsilea*

A, *B*, stages in the swelling of the part of the sporocarp to which the sori are attached. *C*, a sorus showing megasporangia; the lighter-colored bodies are microsporangia with microspores. *D*, the mucilaginous ring has carried the sori out of the sporocarp. (After Hanstein)

Eusporangiate ferns. There are two small families of eusporangiate ferns, the *Ophioglossaceae* and the *Marattiaceae*. All the eusporangiate ferns are homosporous. In most species of the *Ophioglossaceae* the stem is underground and produces a single leaf at a time with a petiole. From this leaf there arises a stalk which may be a continuation of the petiole, and on which the sporangia are borne (Fig. 924). The gametophyte is mostly subterranean, and is saprophytic, as in *Lycopodium*.

The *Marattiaceae* are a tropical family containing both small and large forms. In some cases the sporangia are fused into groups called synangia (Fig. 925). The prothallus is an independent green plant, and in some cases is rather large and branched and resembles that of a thallus liverwort.

Leptosporangiate ferns. Most of the modern ferns are included in this group, and it is in them that we find the great variety of vegetative structures mentioned in the introduction to the *Filicineae*. There are two hundred or more genera and some ten thousand species. Most of the leptosporangiate ferns are homosporous, but there is a small group of water ferns which are heterosporous.

In the homosporous leptosporangiate ferns the sporangia are usually arranged in definite groups or sori, but may be scattered over the whole under surface of the leaf. In some cases the sorus is without a covering; in others there is a thin membranous covering known as an indusium (Fig. 822). In some the sporangia occur in longitudinal lines near the margin of the leaf and the edge of the leaf is rolled over to form a false indusium (Fig. 828). The leptosporangiate ferns are divided into families which are based largely on the general character of the sporangia and the nature of the annulus. In all of the homosporous leptosporangiate ferns the prothallus is a small, thin independent green plant.

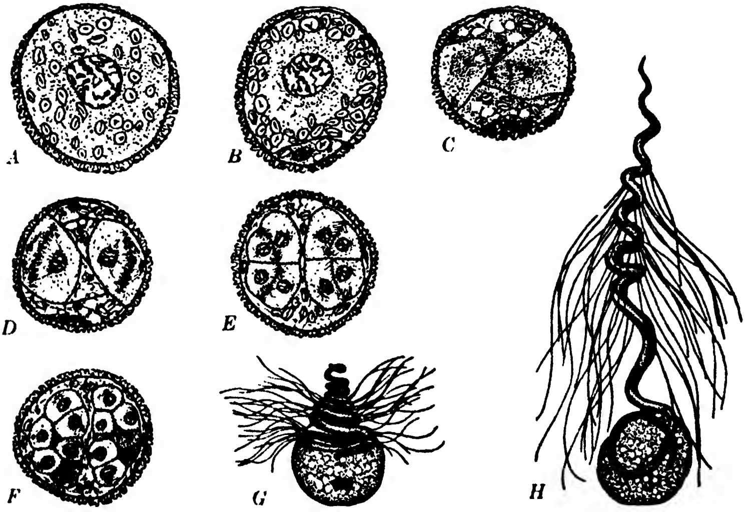


FIG. 929. *Marsilea*

A, microspore; *B*, microspore in which the small prothallial cell seen in the lower part of the microspore has been formed; *C–F*, stages in the development of the two antheridia (note the disappearance of the single prothallial cell); *G*, *H*, spermatozoids. (After Sharp)

✓ ***Marsilea.*** *Marsilea* may be taken as an example of the heterosporous ferns. The stem of *Marsilea* is creeping and branched. The leaves have long stalks, and each terminates with four cloverlike leaflets (Fig. 926). *Marsilea* grows in shallow water or very wet places. When growing in water, the length of the leafstalk varies with the depth of the water. The spores of *Marsilea* are of two kinds, megaspores and microspores. These are formed together within a hard oval structure known as a sporocarp. The sporocarps are borne on short stalks which arise from the lower part of the stalks of fertile leaves (Fig. 926). The sporocarp corresponds to a leaf segment which, by a peculiar method of growth, produces a hard covering within which are numerous sporangia arranged in sori (Fig. 927). The macrosporangia and microsporangia occur in the same sorus (Fig. 928). After a period of rest, the sporocarps germinate when placed in water. The part of a sporocarp to which the sori are attached becomes gelatinous and swells, thus carrying the sori outside of the covering of the sporocarp (Fig. 928). Various features of the water ferns, including the method by which the sporangia are formed (Fig. 927), show clearly that the water ferns belong to the modern fern, that is, the leptosporangiate ferns.

As in *Selaginella*, a male gametophyte develops within a microspore. This consists of one or two prothallial cells and two antheridia (Fig. 929). A single archegonium is formed at one end of a megaspore, which thus becomes the female gametophyte (Fig. 930).

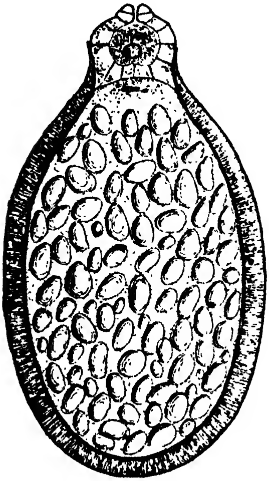


Fig. 930. Female gametophyte of *Marsilea*

Note that a single very large cell with numerous starch grains practically fills the megaspore and that at the end of this cell there is a single archegonium which projects from the spore wall

Interrelationship of *Pteridophyta*. In the early Devonian there appeared the most primitive of the known orders of *Pteridophyta*, the *Psilophytales*. Before the close of the Devonian the *Psilophytales* seem to have disappeared, but before they did so they had given rise to three prominent and distinct lines of evolution: the *Equisetineae*, the *Lycopodiineae*, and the *Filicineae* (Fig. 1037). The *Equisetineae* and *Lycopodiineae* developed rapidly and were dominant plants in Carboniferous time. Before the dawn of the Mesozoic they declined greatly, and soon sank to an unimportant position such as they occupy at present. The *Filicineae* developed much more slowly, and did not come into great prominence until the Mesozoic. They have continued to develop, and are probably more important constituents of the flora of the present than at any time in the past.

CHAPTER XXVIII

DIVISION *SPERMATOPHYTA*

General characteristics. The *Spermatophyta*, or seed plants, are distinguished from all others by the possession of seed. In the *Spermatophyta* the familiar seed plant is a sporophyte. The sporophytes of this group are the most complex of all plants, and among them are found the classes of plants which are generally regarded as the culmination of the evolutionary processes in the plant kingdom. In the *Spermatophyta* the sporophyte reaches its highest development. In the bryophytes the sporophyte is small and dependent on the gametophyte. In those forms with the simplest sporophytes this dependence is complete, while in the *Anthocerotales* the sporophyte is partially self-sustaining, as it has assimilative tissue with chlorophyll. In the *Pteridophyta* the sporophyte is dependent on the gametophyte only during its early stages, and in homosporous forms the mature sporophytes and gametophytes are both independent plants; there are thus two independent generations. In the heterosporous pteridophytes, sporophytes and gametophytes are still separate plants; but the gametophyte is reduced and is dependent for its nourishment on food derived from the sporophyte. In the *Spermatophyta* the gametophytes lose their independence entirely: they are nourished by the sporophyte and develop within the sporophyte. The spore which gives rise to a female gametophyte is surrounded by the tissue of the parent sporophyte during its entire existence, and so is the gametophyte itself. We find thus that the relative importance of sporophytes and gametophytes is the reverse of the condition found in the simpler bryophytes. Within the *Spermatophyta* themselves we see a continuation of the development of the sporophyte and a decrease in the development of the gametophyte.

Sporangia and spores. All seed plants are heterosporous in the sense that there are two kinds of spores, one producing male prothalli and the other female prothalli. The two types of spores are very different in appearance and are produced in very different kinds of sporangia, and the prothalli which are developed from them are very dissimilar. The terms "megaspores" and "microspores" which are used in the *Pteridophyta* are also applied in the *Spermatophyta* to spores which produce respectively female and male prothalli. The names are misleading in that there are no such differences in size among the spores as between the megaspores and microspores of the *Pteridophyta*, the microspores of the *Spermatophyta* being often larger than the megaspores. As the important difference is not one of size but of the sex of the prothalli produced, the terms "gynospores" and "androspores" are more appropriate.

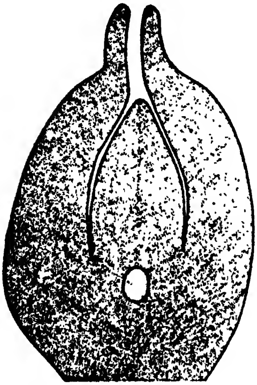


Fig. 931. Longitudinal section through ovule of *Cycas rumphii*

The ovule consists of the nucellus surrounded by an integument; within the nucellus is a young, rounded female prothallus. (× 20)

In *Spermatophyta* the androspores, or microspores, are known as pollen grains, and the sporangia in which they are produced as pollen sacs. The gynosporangium, or megasporangium, is the ovule.

The spermatophytes are divided into two classes, gymnosperms and angiosperms. In the angiosperms the ovules are enclosed in ovaries; in the gymnosperms they are exposed as they are in the pteridophytes.

Ovule and female gametophyte. The ovule consists of a central mass, the nucellus, or sporangium proper, enclosed in one (Fig. 931) or two envelopes called integuments. The integuments arise as collarlike outgrowths which grow up over the nucellus and enclose it completely except at the apex, where there is a small opening, the micropyle (Figs. 325, 931). A spore mother cell is formed within the nucellus (Fig. 932). In most species there is only one spore mother cell, but in some cases there are more. Typically the spore mother cell divides to form a row of four spores (Fig. 932). Three of these degenerate, while the remaining one germinates (Fig. 932)

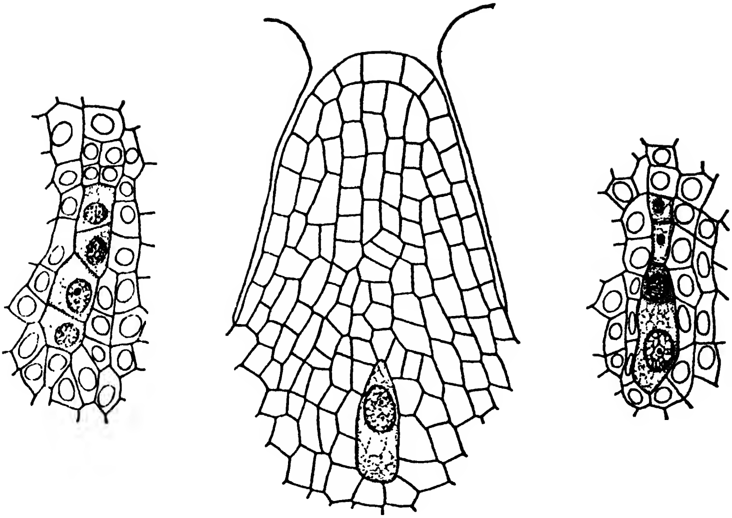


Fig. 932. Spore mother cell and spores in ovule of *Zamia floridana*

Center, spore mother cell within the nucellus, the curved lines outside the nucellus showing location of the integument; left, four spores formed by the division of the spore mother cell; right, the three apical spores have begun to disorganize, while the lowest, which will give rise to the female prothallus, is enlarging. (Redrawn after F. Grace Smith)

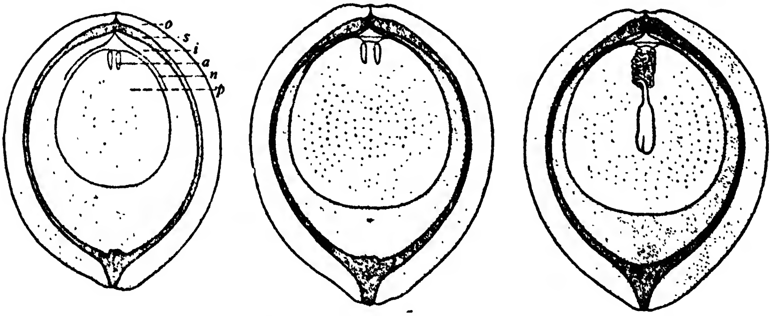


Fig. 933. Longitudinal section through ovule and seed of *Cycas rumphii*

Left, ovule some months before fertilization; *o*, outer layer of the integument; *s*, stony layer of the integument; *i*, inner fleshy layer of the integument; *n*, nucellus; *p*, female prothallus; *a*, archegonium. Center, an older ovule; the prothallus has enlarged, while the nucellus has largely disappeared. Right, an embryo has grown from one of the archegonia and penetrated into the prothallus. ($\times \frac{10}{13}$)

and produces a female gametophyte, or prothallus, which remains permanently enclosed within the sporangium (Fig. 933). In most of the gymnosperms archegonia are produced at the micropylar end of the prothallus, but in the angiosperms there are no archegonia and one of the cells of the prothallus becomes an egg.

Pollen sacs and pollen. The pollen grains are borne in sporangia on sporophylls (Fig. 934) which are called stamens. In most of the gymnosperms the pollen grains are carried by the wind, and by chance some are deposited at or in the micropyle (Fig. 997) of an ovule. The pollen grain sends out a pollen tube that grows through the nucellus toward the archegonia (Fig. 999). The eggs in the archegonia are fertilized either by spermatozoids or by male nuclei from the pollen tube. In the angiosperms, where the ovules are enclosed in an ovary, the pollen grains are deposited on the stigma, and the pollen tube grows through the style before reaching the ovule (Fig. 326).

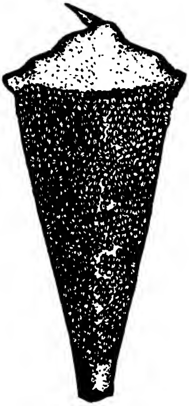


Fig. 934. Under surface of staminate sporophyll of *Cycas rumphii*, showing many pollen sacs. (× 1½)

Seed. The fertilized egg germinates and produces an embryo which is enclosed within the tissue of the ovule. The embryo together with the surrounding tissue of the female gametophyte and of the ovule (Fig. 933), or of the ovule alone, is known as a seed. The seed is the characteristic structure of the division *Spermatophyta.* In the angiosperms the nucellus almost completely disappears during the growth of the seed.

CLASS *GYMNOSPERMAE*

The class *Gymnospermae* is the more primitive of the two classes of the *Spermatophyta,* and is characterized by ovules which are not enclosed in ovaries. The term "enclosed" is used in the sense of being surrounded by a continuous covering of tissue. It is necessary to distinguish between being enclosed in this way and being hidden and surrounded by a number of different structures. In the pine, for instance, the scales of the cone are so close together until the

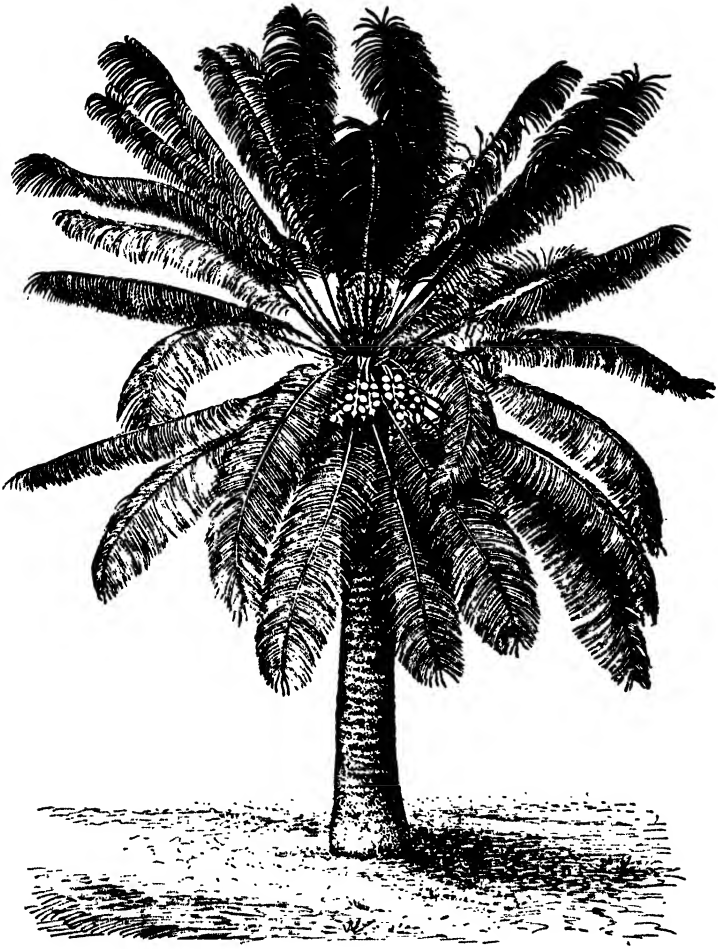


Fig. 935. *Cycas rumphii*

At the apex there is a group of young ovulate sporophylls with ovules slightly past the pollination stage; below the sporophylls is a whorl of foliage leaves; below this is a circle of old sporophylls with nearly matured seeds; below these sporophylls is another whorl of leaves. (× $\frac{1}{28}$)

seeds are ripe that the seeds are completely surrounded and hidden from view. However, the scales are never actually united but simply in close contact. When the cone opens it does so by the spreading apart of the scales. In angiosperms the fruit opens by actual splitting or by the breaking down of the covering, and not simply by the separation of distinct parts.

In the pine the scales not only separate when the seeds are ripe, but also at the time of pollination, so that there is an opening by which the pollen can reach the ovules. In the angiosperms, as was shown in an earlier chapter, at the time of pollination the ovules are enclosed in an ovary, the pollen grains are deposited on a stigma, and the pollen tube must go through the tissue surrounding the ovules in order to reach the latter.

In the structure of the vascular elements gymnosperms are more primitive than are angiosperms. In the larger and more primitive orders of the gymnosperms the wood is composed of tracheids and wood parenchyma and does not contain wood fibers or vessels. Companion cells are not found in the phloem. As we have seen earlier, the vessels and wood fibers of the angiosperms originated through the specialization of tracheids. The difference in the character of the wood in gymnosperms and angiosperms, and the exposed position of the ovules in the gymnosperms, are features which indicate that the gymnosperms are more primitive than the angiosperms. More complete evidence for this view will be given later. The life history of *Cycas*, the most primitive genus of living seed plants, will serve as an introduction to the *Spermatophyta.*

Life History of *Cycas*

Sporophyte. The cycads are a small group of plants with either a columnar (Fig. 935) or a tuberous stem which bears a crown of leathery pinnately compound leaves (Figs. 940, 951). The stems are unbranched or sparingly branched. In the stem there is a relatively large pith surrounded by a band of woody tissue which increases in width by secondary thickening (Fig. 936). A slight development of secondary thickening is found in some ferns, but the cycads are the most primitive living plants that have a great development of secondary wood.

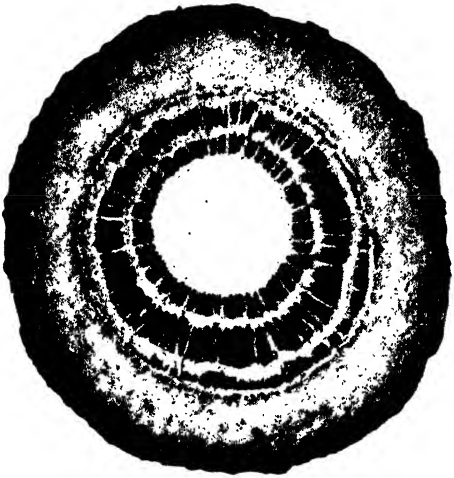


Fig. 936. Cross section of trunk of *Cycas chamberlainii*

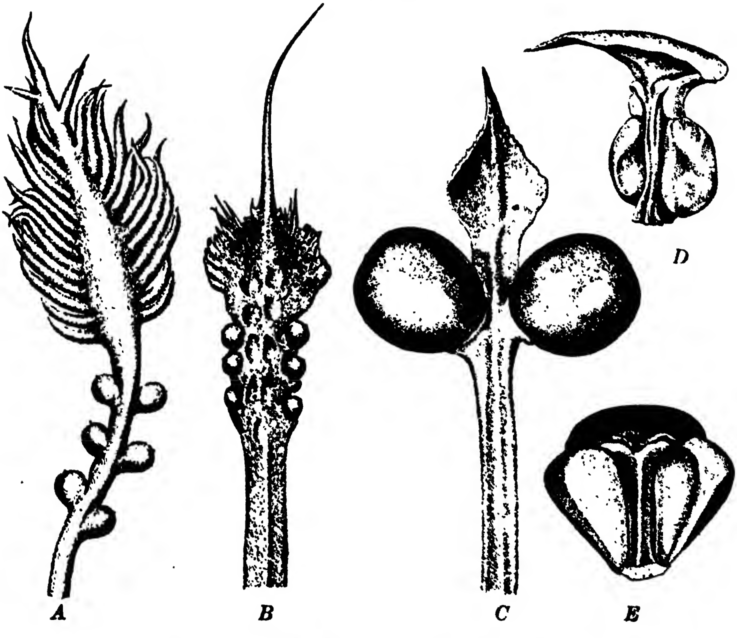


Fig. 937. Ovulate sporophylls of cycads

A, *Cycas revoluta* with young ovules (× $\frac{2}{5}$); *B*, *Cycas circinalis* with young ovules (× $\frac{2}{5}$); *C*, *Cycas rumphii* with seed (× $\frac{2}{5}$). This species usually bears six ovules, but two or four are also frequent. *D*, *Dioon edule* with seed (× $\frac{2}{5}$); *E*, *Zamia* with seed (× $\frac{4}{5}$)

Both the ovules and the pollen sacs are borne on modified leaves, known respectively as ovulate sporophylls (Figs. 935, 937) and staminate sporophylls (Fig. 934). The staminate sporophylls are relatively small, bear large numbers of sporangia or pollen sacs on their lower surfaces, and are aggregated into definite cones (Figs. 938, 939, 940) produced at the apex of the stem. In all the genera except *Cycas* the ovules also occur in a cone (Fig. 941) at the apex of the stem. In the genus *Cycas* the ovulate sporophylls are not in cones (Fig. 935) and are somewhat similar to ordinary leaves (Fig. 937); they are produced at the tip of the stem in whorls alternating with whorls of ordinary leaves (Fig. 935). The ovulate sporophylls of *Cycas revoluta* are very leaflike in appearance (Fig. 937), while those of the genus *Zamia* bear almost no resemblance to ordinary leaves; between these two extremes there are various gradations (Fig. 937). The leaflike appearance of the ovulate sporophylls of *Cycas revoluta* indicates

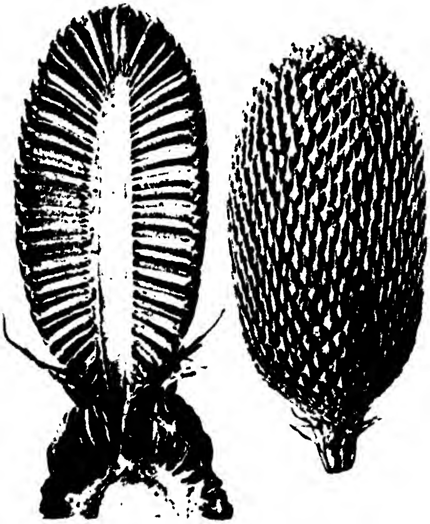


Fig. 938. Cone of staminate sporophylls of *Cycas*

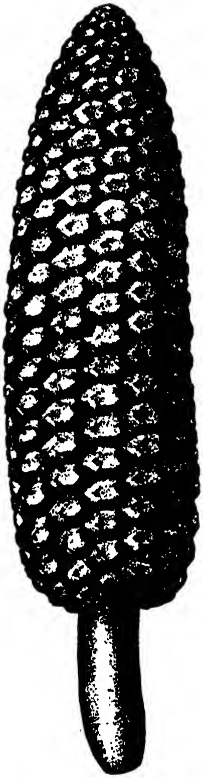


Fig. 939. Cone of staminate sporophylls of *Zamia floridana*. (× 1)

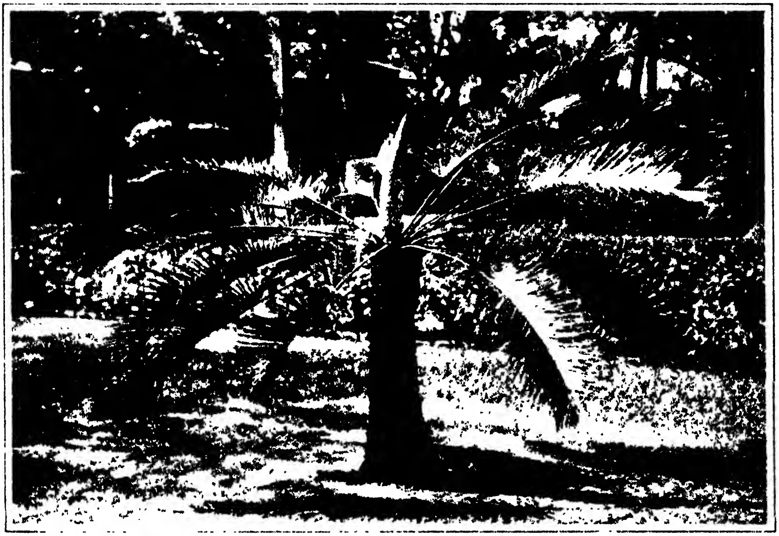


FIG. 940. *Cycas* with staminate cone

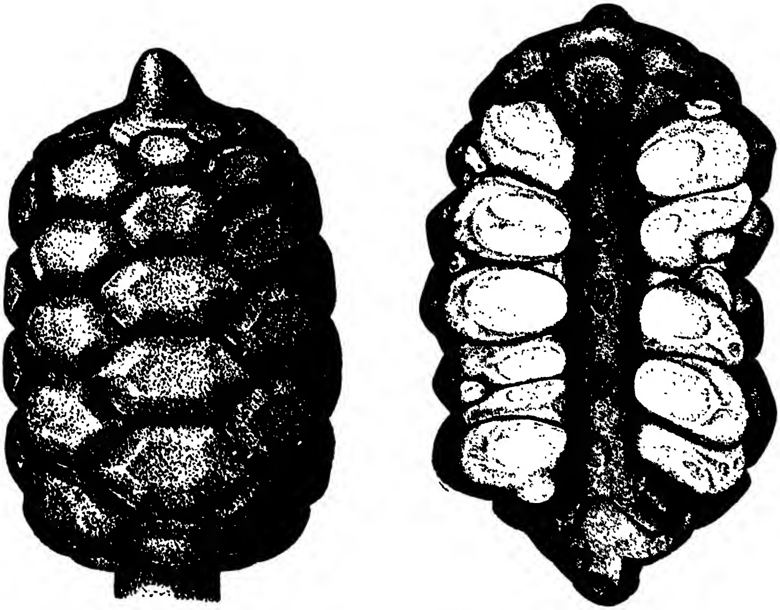


FIG. 941. Cone of ovulate sporophylls of *Zamia floridana*

Left, entire cone; right, cone with some sporophylls removed and showing seed. (× $\frac{2}{3}$)

that they have been derived from ordinary spore-bearing leaves, and the gradations between the ovulate sporophylls of *Cycas revoluta* and those of *Zamia* indicate that even the highly modified sporophylls of *Zamia* had a similar origin.

Ovule and female prothallus. In the cycads the ovule consists of the nucellus, or sporangium proper, and a single integument enclosing the nucellus, except that at the apex there is a small opening, the micropyle (Fig. 931). Within the nucellus there is produced a spore mother cell which divides to form a row of three or four spores (Fig. 932). All except one of these degenerate and disappear, while the functional spore germinates within the nucellus (Fig. 932) and produces a large oval female prothallus (Figs. 931, 933). This prothallus is retained permanently within the nucellus.

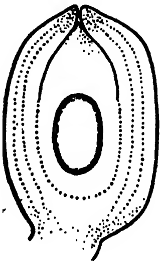


Fig. 942. Longitudinal section through ovule of *Ceratozamia longifolia*

In the center is a developing prothallus. At this stage it is multinucleate without cross walls, and the protoplasm with the nuclei lines the spore wall. (× 10). After Treub

The first division of the spore nucleus is without the formation of cross walls. This is also true of several succeeding divisions. This method of division is known as free nuclear division, and the result is that there are quite a number of nuclei which lie free in the cytoplasm of the growing prothallus. At a very early stage a large central vacuole appears in the cytoplasm, so that the nuclei lie in a peripheral layer of cytoplasm which lines the spore wall (Fig. 942). After the nuclei have become numerous, walls are formed. The wall formation appears first at the periphery and proceeds progressively inward until the prothallus becomes cellular.

As the prothallus matures it produces archegonia, which are usually in a group below the micropyle (Figs. 933, 943, 944). The archegonium of the cycads consists of two neck cells and a large egg cell (Fig. 944). The neck canal cells found in bryophytes and pteridophytes are lacking, while the ventral canal cell is represented by an evanescent nucleus which, with the surrounding cytoplasm, disorganizes soon after its formation (Fig. 945). This evanescent nucleus appears to have no function, but represents the survival of an ancestral characteristic.

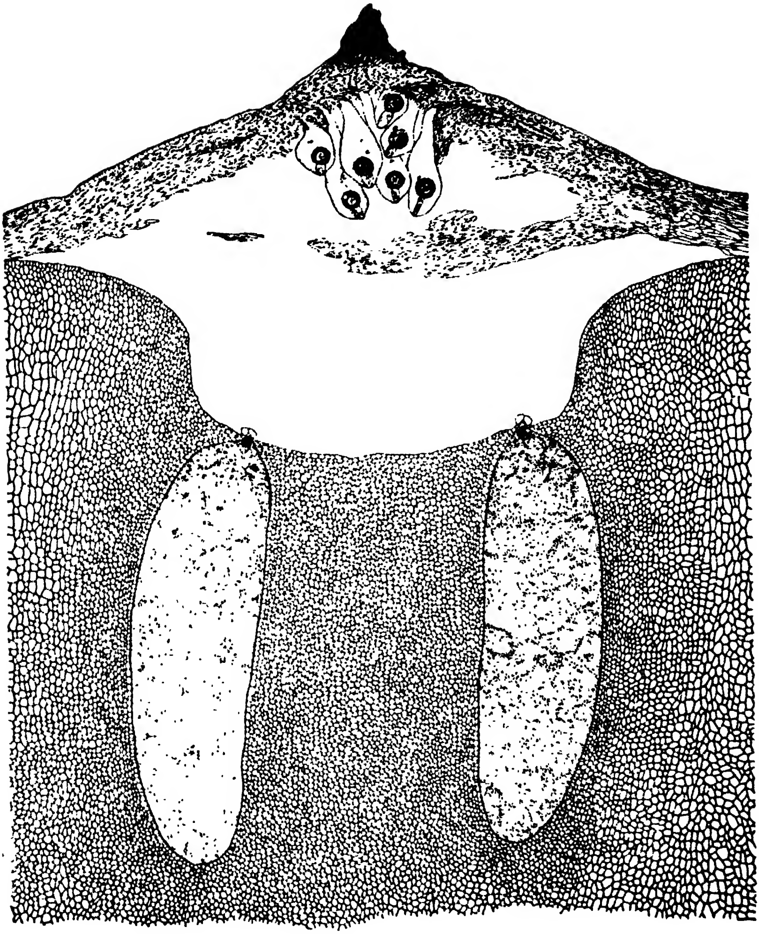


Fig. 943. Longitudinal section of apical portion of ovule of *Cycas rumphii* shortly before the time of fertilization

Above is the nucellus, through which pollen tubes are growing; below is a portion of the female prothallus, showing two archegonia

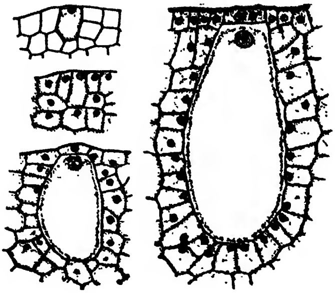


FIG. 944. Development of archegonium of *Dioon*. (× 75)

After Chamberlain

Male prothallus and fertilization. Before being shed the pollen grain germinates and produces a male gametophyte, or prothallus, within the pollen grain (Fig. 946). This gametophyte consists of a sterile prothallial cell, a generative cell, and a tube cell. In this three-celled condition the pollen grains are shed. The pollen grains are carried by the wind and enter an ovule through the micropyle (Fig. 947). Here the pollen tube cell sends out a pollen tube which becomes embedded in the nucellus and, by elongating, carries the prothallial and generative cells through the nucellar region toward the archegonia (Fig. 946). The generative cell

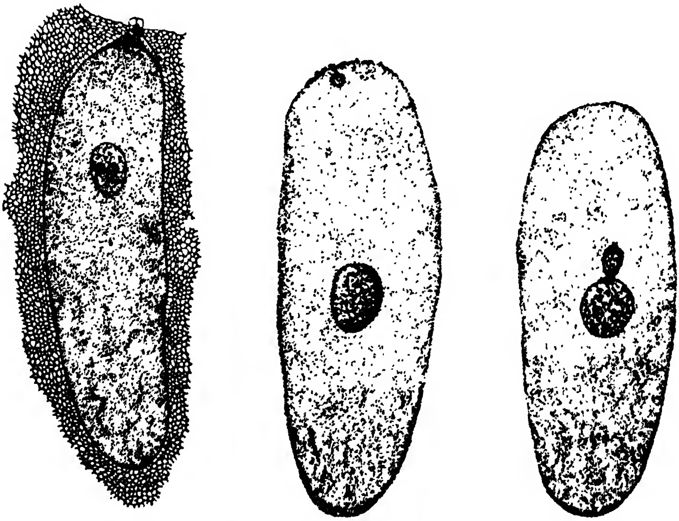


FIG. 945. Archegonia and eggs of *Cycas rumphii*

Left, archegonium in the upper part of which the ventral-canal nucleus and surrounding cytoplasm are disintegrating (× 17); center, an egg into the upper portion of which a spermatozoid has penetrated (× 22); right, an egg with the nucleus of the spermatozoid about to fuse with the egg nucleus (× 22)

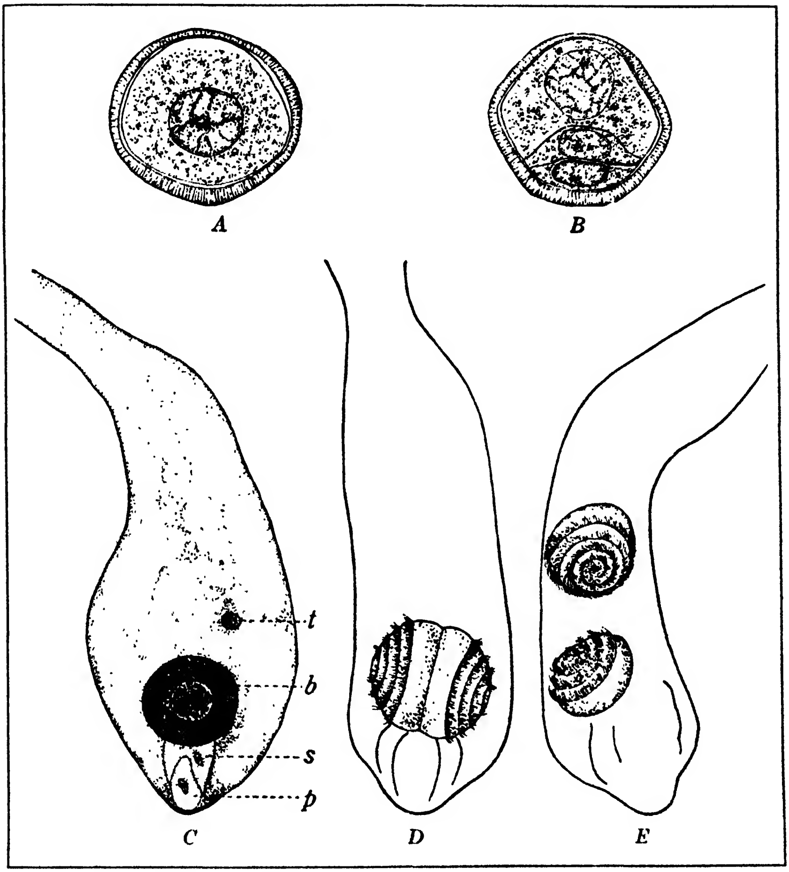


Fig. 946. Pollen grains and pollen tubes of *Cycas rumphii*

A, pollen grain before division of nucleus (× 1080). *B*, pollen grain after the formation of male prothallus; above is the large tube cell, below this the generative cell, below the generative cell the prothallial cell. *C*, pollen tube before division of body cell (× 47); *t*, tube nucleus; *b*, body cell; *s*, stalk cell; *p*, prothallial cell. *D*, pollen tube in which the prothallial cell and stalk cell are disappearing and in which the body cell has divided to form two spermatozoids. *E*, an older stage showing the two spermatozoids. (Last two drawings after Miyake)

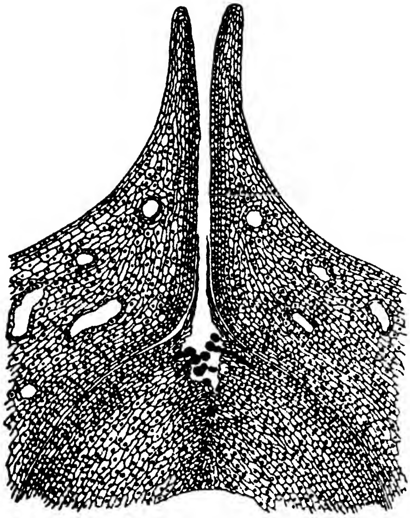


FIG. 947. *Bowenia*

Section of upper portion of ovule showing integument surrounding nucellus. In the upper part of the nucellus there is a cavity, the pollen chamber. Pollen grains are seen germinating in the pollen chamber. (After Lawson)

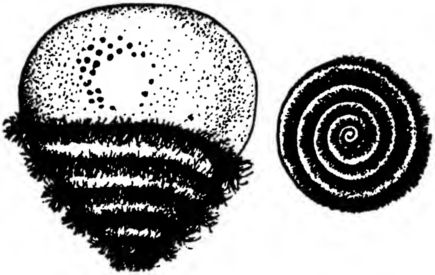


FIG. 948. Spermatozoid of *Zamia floridana*

Left, side view (× 125); right, apex of spiral. (After Webber)

later gives rise to a sterile stalk cell and a large body cell (Fig. 946). The latter produces spermatozoids (Fig. 946). These are large flagellated structures which have the ability to swim (Fig. 948). The pollen tube approaches the archegonium and discharges the spermatozoids, one of which enters the archegonium and fuses with the egg cell.

The flagellated spermatozoids in a highly developed land plant show the survival of a character acquired by aquatic ancestors.

Seed. The fertilized egg develops and produces an embryo which remains embedded in the prothallus (Figs. 933, 949). The fertilized egg undergoes a long period of free nuclear division similar to that of the prothallus. In this way a proembryo is formed (Fig. 950). A conspicuous mass of cells is formed at the base of the proembryo. The lower of these become the embryo, while those above differentiate into a suspensor. The latter elongates very greatly and carries the embryo down into the prothallus. In mature seeds the suspensor forms a conspicuous structure at the base of the embryo (Figs.

933, 949). The embryo in most genera of cycads has two large cotyledons.

After the embryo reaches a certain size the seed is mature. In the mature seed the embryo is surrounded by the prothallus, and the prothallus is surrounded by the integument, the nucellus having largely disappeared (Figs. 933, 949). The prothallus contains a very considerable supply of stored food. During germination the embryo lives on this supply of stored food until it has developed sufficiently to be independent.

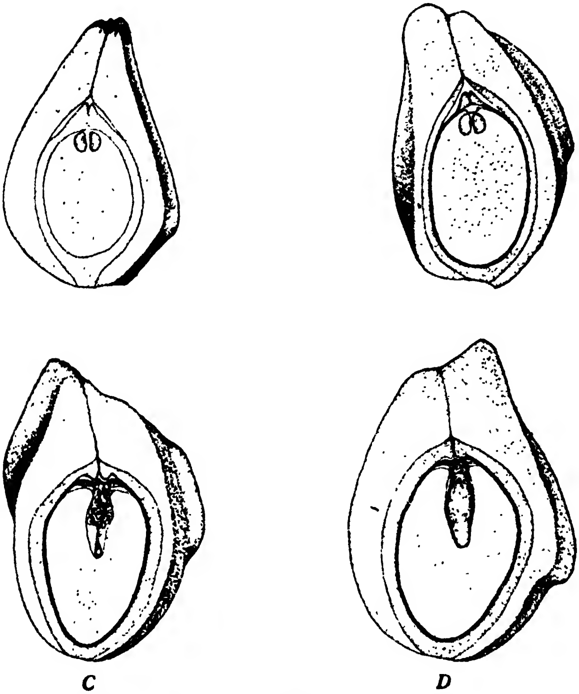


FIG. 949. **Longitudinal section of seed of *Zamia***

A, female prothallus with two archegonia, enclosed in a nucellus, and this within the integument; *B*, older stage in which the nucellus has largely disappeared; *C*, early stage in the development of the embryo (note the long coiled structure, suspensor, which pushes the embryo into the prothallus); *D*, mature seed consisting of embryo surrounded by prothallus and this by the seed coat formed from the integument. The seed coat consists of three layers, a thin fleshy inner layer, a thick stony layer, and a still thicker fleshy outer layer. (× 1½)

Alternation of generations. In the cycads there is an alternation of generations, just as in ferns and in liverworts. In the cycads the

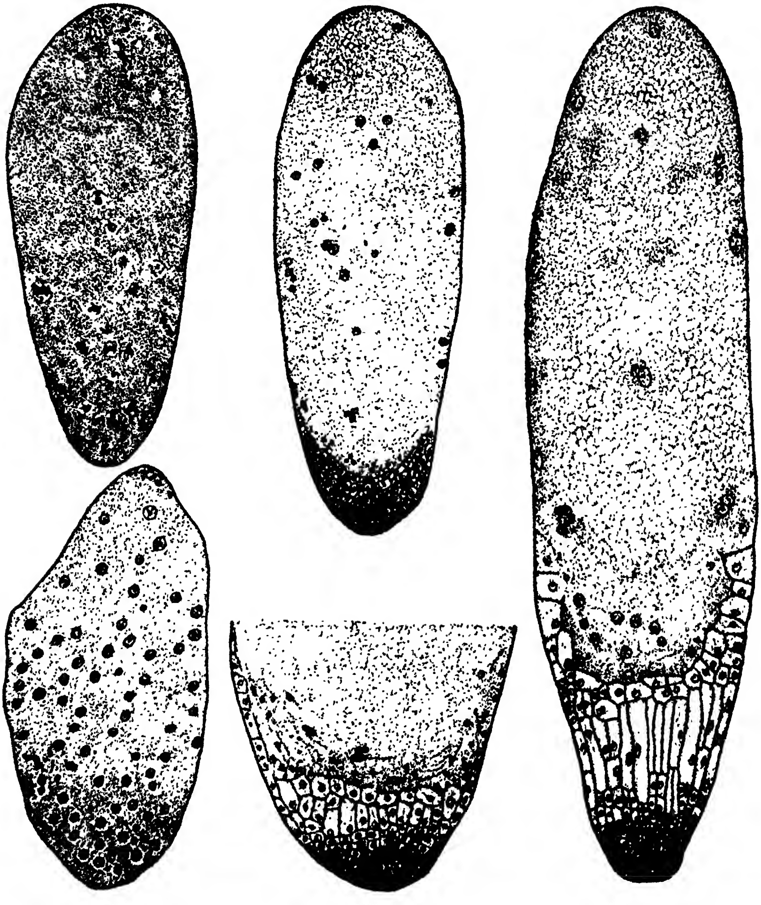


FIG. 950. *Zamia floridana*

Left, free-nuclear stage; center, formation of tissue at base of proembryo; right, suspensor has begun to elongate. (After Coultier and Chamberlain)

sporophytic generation is heterosporous. The spores give rise to the gametophytes. The female gametophyte is a prothallus that is developed within the ovule, while the male gametophyte develops from a pollen grain. Just as in ferns, the number of chromosomes is reduced when a spore mother cell divides to form a tetrad of spores. Therefore the spores and the gametophytes produced by them are haploid, while the diploid number of chromosomes is restored when a sperm nucleus fuses with the egg nucleus. This diploid number persists throughout the life of the sporophyte and is reduced again when a spore mother cell divides to form four spores.

In the cycads the prothallus, or female gametophyte, is retained permanently within the sporophyte, and even the young sporophyte begins its development under the protection of the previous sporophytic generation. Thus the gametophyte, which in the liverworts is the dominant phase and in the ferns is an independent plant, is reduced in the cycads to a condition in which it is parasitic on the sporophyte. On the other hand, the sporophyte is much more highly specialized in the cycads than in any of the pteridophytes.

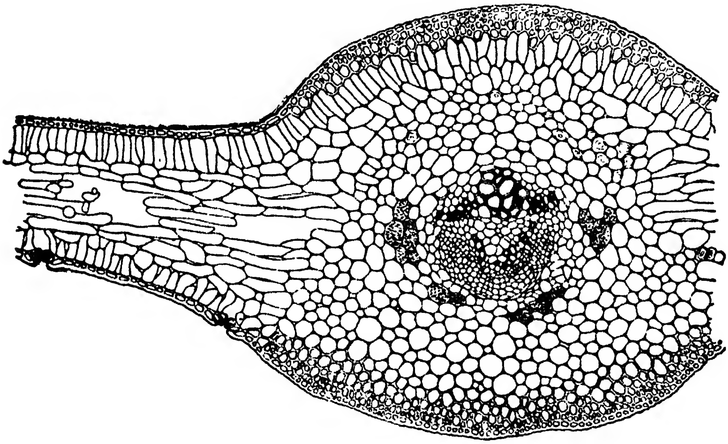


Fig. 951. Cross section of a portion of a leaf of *Cycas*, showing midrib and portion of thin part of blade. (× 50)

Order *Cycadofilicales* (Pteridosperms, or Seed-Ferns)

General characteristics. This extinct order of plants appeared first in the Devonian period, and became very prominent in both species and individuals during Carboniferous times. Some re-

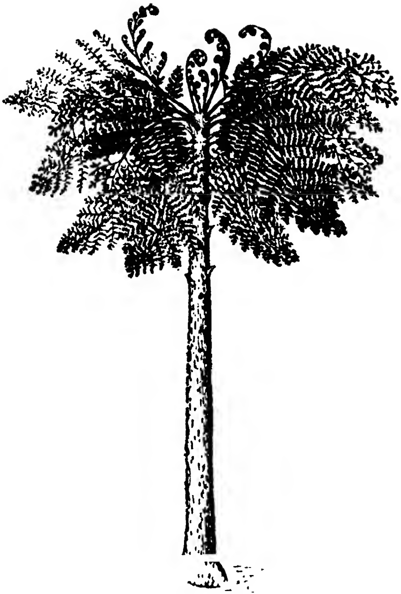


FIG. 952. *Eospermatopteris*, a Devonian seed-fern
After Goldring

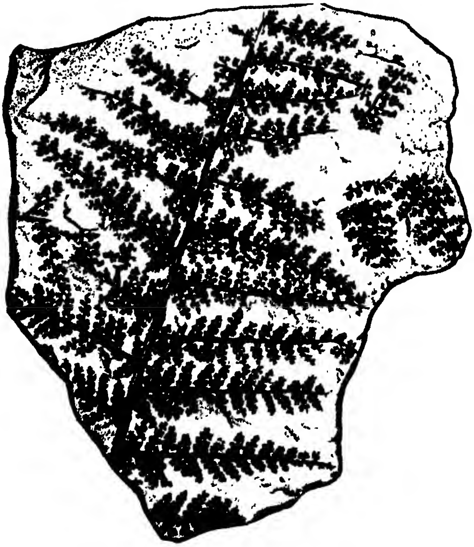


FIG. 953. Portion of leaf of *Lyginopteris oldhamia*
After Schimper

sembled modern tree ferns (Fig. 952) and had moderately tall stems with occasional branches; but many, and probably most, were much smaller. The leaves are so similar to fern-fronds that for a long time they were regarded as such (Fig. 953), and it was only when it was found that seeds were attached to them (Fig. 954) that the *Cycadofilicales* were separated from the ferns and regarded as the most primitive order of the gymnosperms.

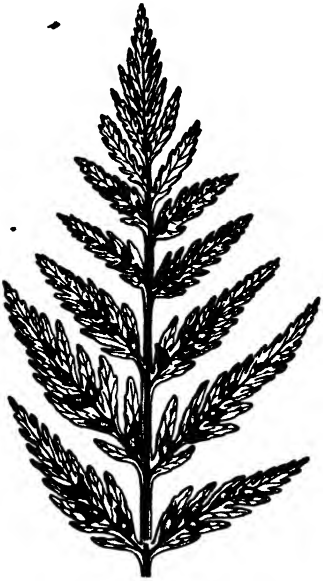


Fig. 954. ***Sphenopteris tenuis*, one of the *Cycadofilicales***

Portion of leaf with seed. (× $\frac{3}{4}$). After Halle

Stems of *Cycadofilicales*. The structure of the stem varied considerably in different genera. In one of the best-known there was a solid stele (protostele) consisting of solid xylem surrounded by phloem, a condition characteristic of many primitive pteridophytes, including some ferns. However, as in other *Cycadofilicales*, a cambium is found between the xylem and the phloem, and this gave rise to a considerable development of secondary tissues in the same way that secondary thickening takes place in higher plants.

One type of stem has a rather modern structure (Fig. 955). There is a central pith surrounded by a ring of vascular bundles which are separated from each other by pith rays. In the bundles the xylem was toward the center and the phloem toward the exterior (Fig. 956), as in modern plants, while between the xylem and phloem was a cambium which gave rise to secondary thickening in the usual manner. These stems resemble cycads in containing much soft tissue and in having a wide central pith. Microscopic details emphasize this similarity and show that while some of the stems with a central pith in *Cycadofilicales* were more primitive than those of the cycads, there were intermediate forms which led up to a typical cycad structure.

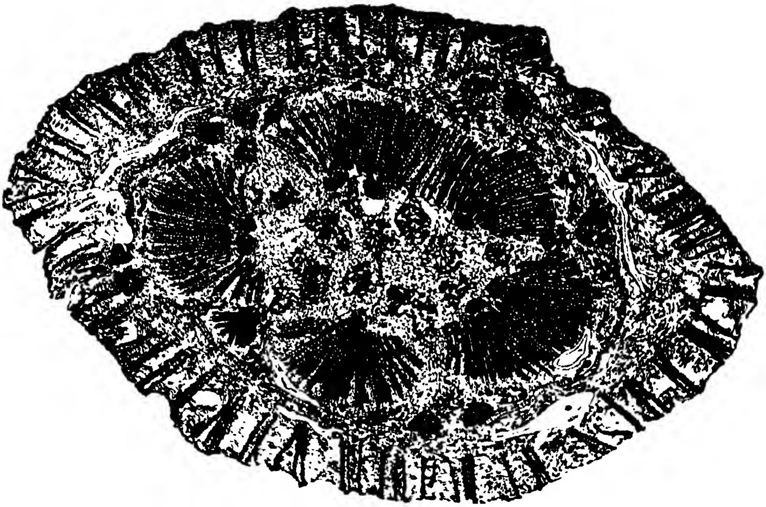


Fig. 955. Cross section of a stem of *Lyginopteris oldhamia*

Note large central pith and considerable development of secondary xylem. The primary xylem is just within the secondary xylem. Note also the wide cortex. (After Williamson and Scott)

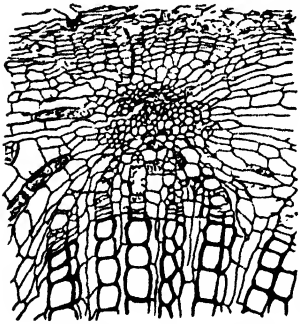


Fig. 956. *Lyginopteris oldhamia*

Cross section of a portion of a vascular bundle with secondary thickening. Below, secondary xylem; next, the cambium followed by secondary phloem, and then the primary phloem. (× 35). After Williamson and Scott

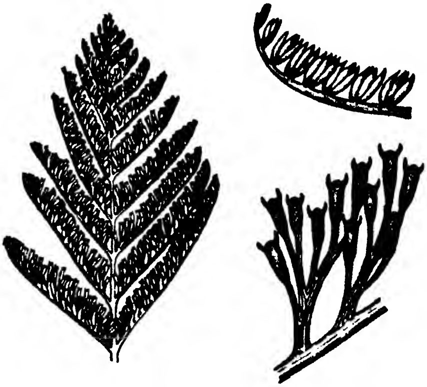


Fig. 957. *Mystroemia pectiformis*

Left, portion of frond with seed (× ¾). Upper right, a small portion of plant with pollen sacs. Lower right, seed. (After Halle)

It was characteristic of a very large group of *Cycadofilicales* that the stem had several steles, each with well-developed secondary thickening.

Reproduction of *Cycadofilicales*. On the fronds of *Cycadofilicales* are found two kinds of reproductive structures; pollen sacs (Fig. 957) and seed.

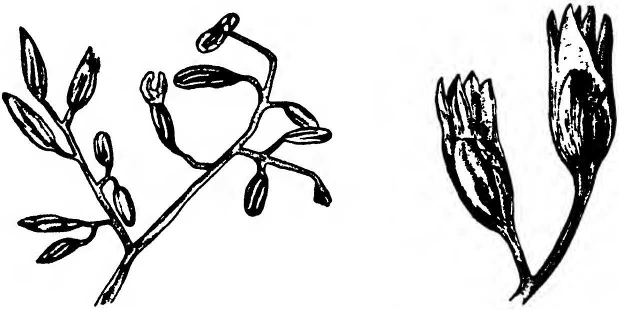


FIG. 958. ***Lagenostoma sinclairi***

Small portion of frond with seeds within sterile coverings, the cupules. (Left, × 1; right, × 2)

The pollen sacs were borne in groups on the fronds, and resembled the sporangia of some ferns (Fig. 957). The pollen sacs, or sporangia, and the spores they contained are indeed so like those of ferns as to leave no doubt that they were derived from fernlike sporangia and spores. However, as the development of the spores resulted in the fertilization of the seed, it is logical to call the sporangia "pollen sacs" and the spores "pollen grains."

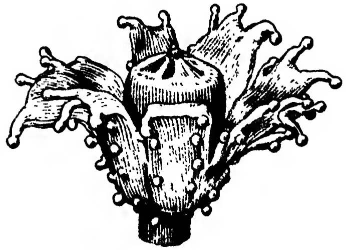


FIG. 959. Seed of *Lyginopteris oldhamia* surrounded by cupule

Note the glands on the cupule. (After Oliver and Scott)

The seeds were also borne on the fronds, on leaflets or replacing them, and were similar in structure to those of the cycads. In many cases the seeds were surrounded by a separate loose covering (Figs. 958, 959). In the seed was a nucellus (sporangium) enclosing a large prothallus (Fig. 960) which, presumably, was derived from a single spore as in the cycads.

Archegonia are found at the apical end of the prothallus (Fig. 961), which is the usual position in gymnosperms. Around the nucellus was an integument which was free from the nucellus in some species (Fig. 961), while in others it resembled that of the cycads in being free from the nucellus only at the tip (Fig. 960). A micropyle, or opening, extended through the tip of the integument; and through this the pollen grains entered the seed.

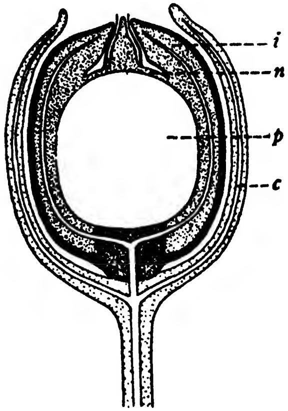


Fig. 960. Longitudinal section through seed and cupule of *Lyginopteris oldhamia*

i, integument; *n*, nucellus; *p*, prothallus; *c*, cupule

Embryos are not found in the seeds in the *Cycadofilicales*, nor in Paleozoic seeds in general. It seems probable that the embryos did not develop until the seeds were shed and ready to germinate. This indicates a primitive condition, because in all living seed plants there is an embryo embedded within the seed.

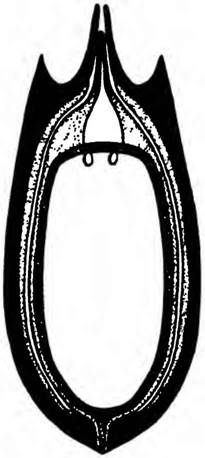


Fig. 961. Longitudinal section of seed of *Stephanospermum akenioides*

In the center is a large prothallus with two archegonia at its apex. Above the archegonia the large pollen chamber in the nucellus is seen. The integument is composed of two layers; it is separate from the nucellus clear to the base of the seed

In the apical end of the nucellus was a cavity known as the pollen chamber (Figs. 961, 962). This varied in form in different genera. Pollen chambers are also found in living cycads (Fig. 947). The pollen grains lodged in the pollen chamber and, apparently, increased in size (Fig. 962). In these pollen chambers there have been found pollen grains containing a number of cells separated from each other by distinct walls, indicating the formation of an antheridium in the pollen grain, as is the case in the microspores of heterosporous pterido-

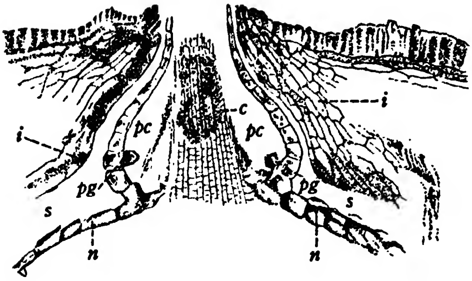


Fig. 962. Tip of the integument and nucellus of *Lyginopteris oldhamia*

i, integument; *s*, space between integument and nucellus; *n*, nucellus; *pc*, pollen chamber; *pg*, pollen grain; *c*, column of nucellar tissue projecting into pollen chamber. (After Oliver)

phytes. Even bodies which may have been spermatozoids have been found in some pollen grains. Altogether it seems probable that the *Cycadofilicales* had motile spermatozoids, as do cycads and *Ginkgo*, but that these did not develop in pollen tubes but in antheridia within the spores or pollen grains, as in the heterosporous *Pteridophyta*. In this respect the *Cycadofilicales* were more primitive than any living seed plant.

Lyginopteris oldhamia. The best-known of the *Cycadofilicales* is *Lyginopteris oldhamia* (Fig. 963), all parts of which have been thoroughly studied. *Lyginopteris* was a fernlike plant with stems which reached a diameter of about four centimeters. The leaves were large, sometimes a meter or more in length. The stem was evidently erect, since the leaves were arranged spirally. The stem was so slender that it is doubtful if it was strong enough to support the plant, so it is

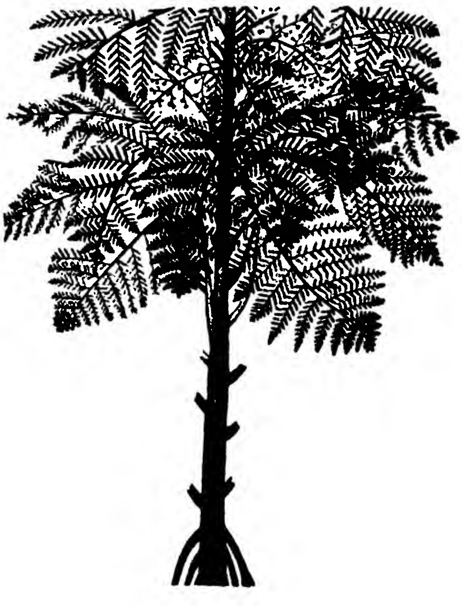


Fig. 963. ***Lyginopteris oldhamia***

After Berry

presumed that *Lyginopteris* scrambled up through other vegetation which helped to support it. The stem had a rather wide pith surrounded by vascular bundles in which there was secondary thickening (Fig. 955). The whole arrangement, including the vascular bundles (Fig. 956), had a rather modern aspect. The seeds were surrounded by a loose sterile covering or cupule (Fig. 959). Stalked glands are found on the stems, leaves, and cupules (Fig. 959). The presence of these characteristic glands has been very convenient in enabling paleobotanists to identify isolated parts of *Lyginopteris oldhamia*. In the center of the seed itself is a large prothallus (Fig. 960), which was surrounded by a nucellus, and this by a single integument. As in modern cycads, the nucellus and integument were fused except at the apex. The tip of the nucellus formed a pollen chamber, which was ring-shaped in form owing to the presence of a central column of nucellar tissue which projected into the pollen chamber and extended out of the micropyle (Figs. 959, 960). The pollen sacs (Fig. 964) were borne on leaves, and had a structure very similar to that of the synangia of some of the modern ferns belonging to the *Marattiaceae*.

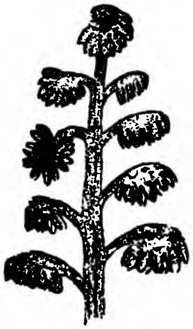


Fig. 964. Portion of a frond of *Lyginopteris oldhamia*

Showing the manner in which the pollen sacs were borne. (After Zeiller)

Relationship of *Cycadofilicales*. As the *Cycadofilicales* are so fernlike in many respects, it was natural that at first they were regarded as ferns which had developed seed. However, as far as geological evidence goes they seem to have been as ancient as the ferns. Moreover, there are anatomical features by which paleobotanists believe that they can distinguish between the stems of ferns and of the *Cycadofilicales* even when the reproductive structures are not known. Thus, while the great similarity of the ferns and *Cycadofilicales* would seem to indicate that these two groups are descended from the same stock, it may well be that the separation took place before the development of the combination of characters which we associate with ferns. If this was the case, the great similarity between the fronds of ferns and those of *Cycadofilicales* was due to the development of two related groups along parallel lines. That this may have been so is indicated by the fact that the fronds of the oldest known *Cycadofilicales* did not have expanded blades, so typical of later *Cycadofilicales* and ferns, but were composed of branched rachises with practically no lamina. A similar absence of lamina was characteristic of the earliest ferns.

The *Cycadofilicales* occupy much the same position among gymnosperms that the *Psilophytales* do in the pteridophytes. They are known further back in geological time than any other gymnosperms, and their remains give us our best idea of a generalized group from which other orders of gymnosperms appear to be descended.

Origin of the seed habit. It appears to be evident that an ovule is a transformed sporangium, and that seed originated through the germination of a spore and the development of a prothallus within the sporangium. In the simplest of the living seed plants the spore is one of a tetrad, and presumably this was true of the seeds of the *Cycadofilicales*.

There are two theories as to the manner in which a sporangium became transformed into an ovule. Until recently it was very generally held that the ovule is a modified megasporangium and that the spore which produces the female prothallus in the ovule is a megaspore. According to this theory the ancestors of the *Cycadofilicales* went through a heterosporous stage somewhat like that of *Selaginella*; specialization went further, however, and only one megaspore in a tetrad developed. This condition is found in some of the ancient lycopods and also in modern water ferns. The germination of a single functional megaspore in a modified megasporangium resulted in the ovule.

In favor of the idea that seeds resulted from a further development of such heterospory as we see in the *Pteridophyta* are the facts that heterospory developed independently in *Equisetineae*, *Lycopodiineae*, and *Filicineae*; that the pollen grains of the *Cycadofilicales* appear to have germinated in much the same way as microspores of the *Pteridophyta*; and that in some of the Paleozoic lycopods megasporangia developed into seedlike structures. The strength of this argument lies in the fact that it shows a method by which seedlike structures were actually produced in the past. Its weakness is that it is based on analogy with what happened in other groups, and not on a consideration of what occurred in the ancestry of seed plants.

The failure to find large and small spores in the ancestry of the seed plants or in the seed plants themselves led to the other theory, according to which the seed habit originated through the germination of homosporous spores within the sporangium, and the ancestors of seed plants had neither megasporangia and microsporangia nor megaspores and microspores. At first many spores started to germinate in a sporangium, in much the same way as do ordinary fern spores. Gradually, through specialization, the number of spores in certain sporangia was reduced, and the type of prothallus changed. Finally only one spore germinated in the ovule, and this produced a large ovoid prothallus. Such a course of events would really have been very similar to the specialization of megaspores. Instead of the spores' becoming larger and storing more food as they became fewer, the protoplast would, as the spores became fewer, have divided to form a mass of cells in which the food was stored. It is largely a question of whether the protoplast of the spore divided after the storage of food as in *Selaginella*, or before or during the process as in living gymnosperms.

Ideas as to the development of pollen grains are the same in both theories. They went through much the same course of evolution as the microspores and male prothalli of the heterosporous *Pteridophyta.*

There are a number of points advanced in favor of the view that the ovule is a modification of a sporangium which produced ordinary-sized spores and not megaspores. In some modern homosporous ferns there is a tendency for the germination of the spores to begin in the sporangium, and germinating spores have been found in the sporangia of very ancient ferns. Living seed plants do not have megaspores and microspores in the sense that they are large megaspores and small microspores. The "microspores" are larger than the "megaspores" about as often as they are smaller. The seed plants seem to be clearly descended from the same common stock as the ferns, and in this stock heterospory is known only in the small, highly specialized, and comparatively recent group of water ferns. On the other hand, heterospory was well developed in Carboniferous *Equisetineae*, and the Carboniferous lycopods were predominantly heterosporous. If seeds are the development of heterospory, it is strange that they evolved in a predominantly homosporous line, and not in the lycopods, where heterospory was the rule.

There appear to be fundamental differences other than size between typical megaspores and the spores which produce prothalli in the ovules of seed plants. The true megaspore, such as that of *Selaginella*, is densely packed with reserve food and is surrounded by a thick wall which prevents any great increase in size or further absorption of food from the sporangium. Neither of these specialized features is found in the spores of ovules; here the spore wall remains relatively thin, and, instead of the spore's being packed with food, food continues to be absorbed during the germination of the spore and the growth of the prothallus. To assume that the megaspore of seed plants went through an evolutionary stage in which it resembled that of *Selaginella* requires the assumption of the reversal of the direction of evolution and the loss of the highly specialized characteristics of a true megaspore. In this connection there is a possibility that the development of the seed habit and that of megaspores are the results of two separate lines of evolution, and that the elaboration of the megaspore was not only not a step toward the production of seed but a specialization which rendered such an end very unlikely.

Unfortunately we do not know the actual history of the transformation of sporangia into the seeds of the order *Cycadofilicales*, and so both of the above views rest on circumstantial evidence.

Advantage of seed habit. The process by which food is stored in seed, even in the simplest living seed plants, affords a great advantage over the storage of food in megaspores. In the formation of a seed, food is not stored until after pollination; not, therefore, until there is reasonable certainty of fertilization. On the other hand, there is no such relation in the case of storage of food in megaspores, and so here there would seem to be much waste of food material. The possession of seed enables the *Spermatophyta* to store more food in each of a smaller number of reproductive structures than is the case in the *Pteridophyta* with megaspores. The result is that the young seed plant gets a better start.

Order *Cycadales*

General characteristics. The living cycads are a small group containing nine genera and less than a hundred species. They form a very homogeneous group, and all belong to a single family, the *Cycadaceae*. The cycads made their appearance toward the close of the Paleozoic and were a dominant group during the Mesozoic. During the latter period they were much more diversified than at present, and were represented by several important and very distinct types which disappeared before the close of the Mesozoic. Most of the Mesozoic cycads were so different from their living relatives, and showed such diversity among themselves, that authorities usually place them in one or more separate orders. It will be convenient here to regard all cycads, both extinct and living, as belonging to one order, the *Cycadales*.

Origin of living cycads. In almost all cases in which a fertile shoot (strobilus), corresponding to the cone of living cycads, can with any probability be assigned to a Mesozoic cycadophyte, the arrangement is very different from that of modern forms, and simulates a flower, sometimes very closely. It is generally believed that modern forms belong to an ancient race which may have originated in the Paleozoic, and there is some geological evidence for this view (Fig. 965). However, the belief is based more on their apparently simple structure and the difficulty of deriving them from the common Mesozoic types than on any direct geological evidence. Their ancestors must have been relatively rare in the Mesozoic.

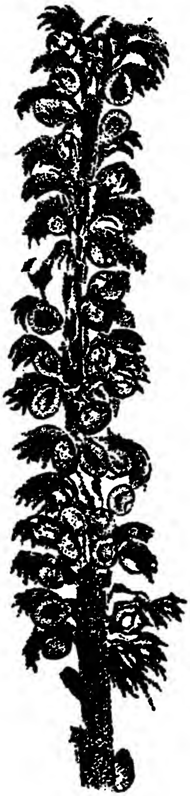


FIG. 965. *Cycadospadix milleryensis*, a Permian fructification suggestive of cycads

This specimen was found in beds which contained cycad-like leaves and a type of stem that shows features intermediate between the general run of *Cycadofilicales* and cycads. It may perhaps represent the fructification of a plant which is on the boundary line between seed-ferns and cycads

It seems certain that the cycads were derived from the *Cycadofilicales*, because the *Cycadofilicales* preceded them in time and because the structure of the *Cycadofilicales* grades into that of the *Cycadales*. We have already noted that the stem structure of some of the *Cycadofilicales* is very similar to that in the cycads. The leaflets of some of the cycads are rolled up circinately when young (Fig. 966), just as in ferns (Figs. 822, 828). In both groups there is dichotomous branching of parallel veins. The ovulate sporophylls of *Cycas* are very evidently modified leaves, and, as has been already noted, there are various gradations between such sporophylls and those which are densely packed in cones and bear little resemblance to ordinary leaves. Except for the presence of embryos in the seeds of cycads, the seeds are remarkably like those of the *Cycadofilicales*.

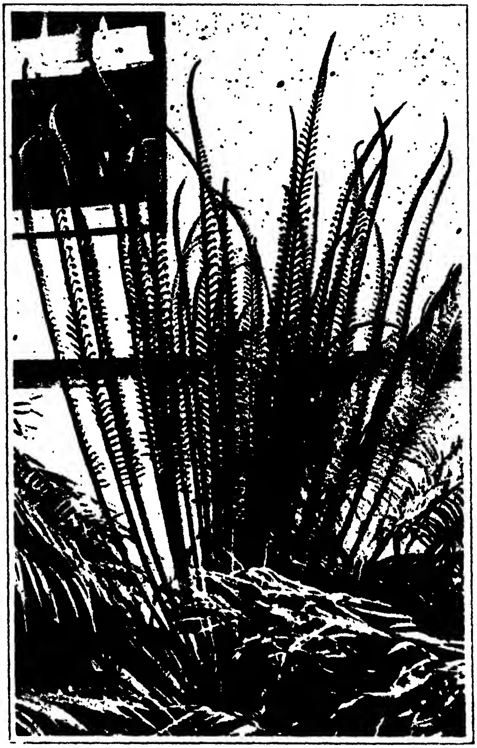


FIG. 966. Young leaves of a *Cycas* showing coiled leaflets

Origin of pollen tubes. The *Cycadales* are the most primitive of all known plants in which the male gametophyte develops a pollen tube. In the cycads the development of the female prothallus stops at a very early stage if pollination does not take place. After pollination there is a very long period during which the female prothallus develops. The male gametophyte undergoes a similar long period of development. In its early stages it sends out a tube which enters the tissue of the nucellus and serves as an absorbing haustorium (Figs. 947, 943). In the *Cycadofilicales* the pollen grains seem to have increased in size while within the pollen chamber, and they may have absorbed food from the nucellus. It seems not improbable, therefore, that the development of pollen tubes may have been initiated as haustoria for the more efficient absorption of food material.

Fossil Cycads

General characteristics. Among the most numerous plants from the Triassic to the lower Cretaceous were the cycadophytes. None of them were of great size. Perhaps none were as large as the tallest of living cycads. The stems of some of the Mesozoic cycadophytes resembled the enlarged ones of modern cycads, but slender branching stems were much more common.

Cycadeoidea. The best known of the Mesozoic cycadophytes belonged to the genus *Cycadeoidea* (Fig. 967). The stems and leaves of these were very similar to those of some of the recent cycads.

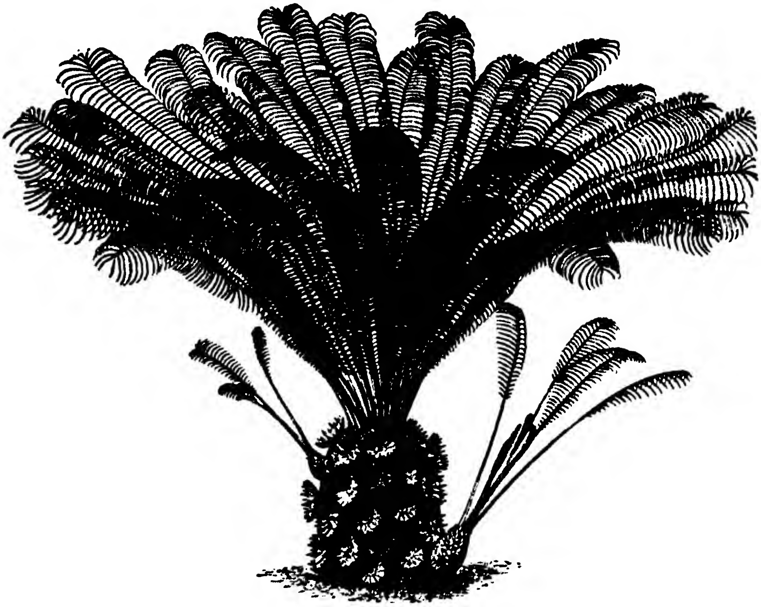


FIG. 967. *Cycadeoidea*

Note the strobili on the large stem

The strobili (fertile branches) were, however, very different; when expanded they must have had a very flowerlike appearance. They were borne in large numbers on the side of the stem (Fig. 967), and not at the tip as in modern cycads. On the lower part of the fertile branch were spirally arranged bracts (Fig. 968). Just beyond these was a whorl of large pinnate stamens with their bases united into a disk (Figs. 968, 969). Beyond these and terminating the branch was a cone, bearing ovules (Fig. 968). In comparing this fertile branch with an angiospermous flower, it will be seen

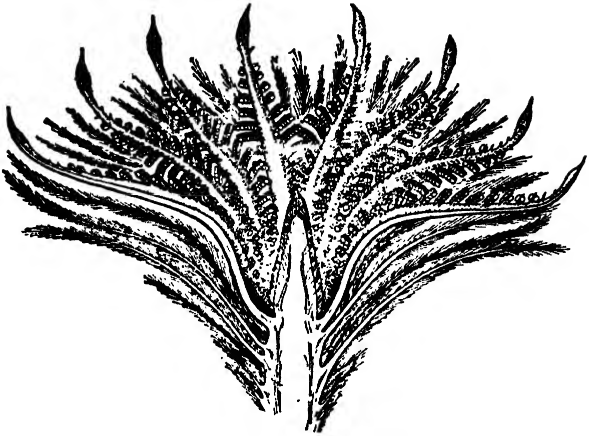


Fig. 968. Longitudinal section of strobilus of *Cycadeoidea ingens* After Wieland

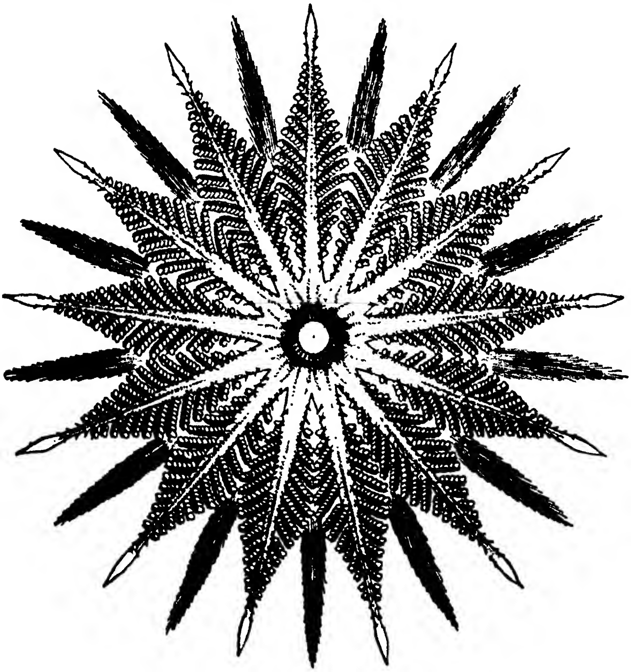


Fig. 969. Top view of strobilus of *Cycadeoidea* The ovulate cone in the center is shown in section. (After Wieland)

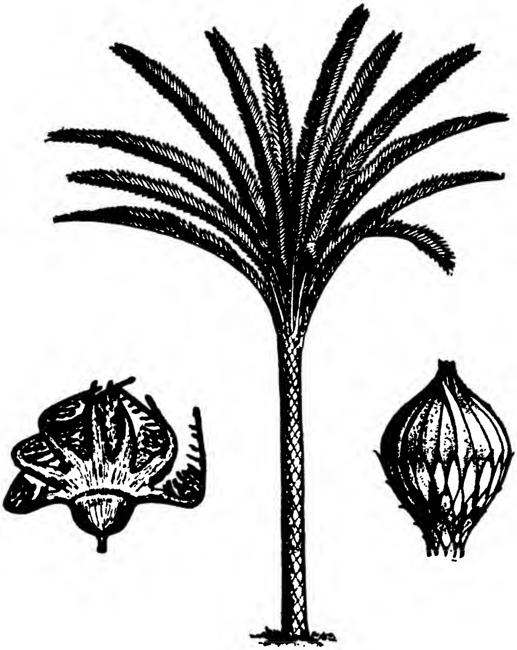


Fig. 972. *Williamsonia gigas*

Center, a plant with two female strobili; lower left, staminate strobilus; lower right, ovulate strobilus. (After Williamson and Thomas)

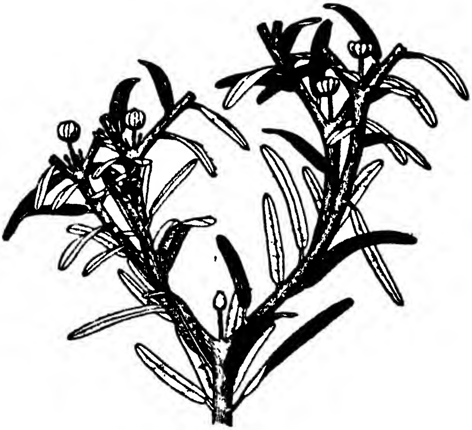


Fig. 973. *Williamsoniella coronata*, a Mesozoic cycad, with leaves and strobili

After Thomas

seminal scales). These were slender pedicels with enlarged tips which spread over the ovules and enclosed them except that the micropyles projected from between the scales (Fig. 970). The seed of *Cycadeoidea* was practically filled by a large embryo with two cotyledons (Fig. 971).

The pollen grains were produced in synangia. A synangium is a group of fused sporangia. In *Cycadeoidea* the synangium consisted of two rows of fused sporangia all surrounded by a layer of thick-walled cells. The synangia were borne on a pinna in two rows, each synangium being attached by a stalk. The structures which at first glance might be taken for sporangia in figures 968, 969, are really synangia.

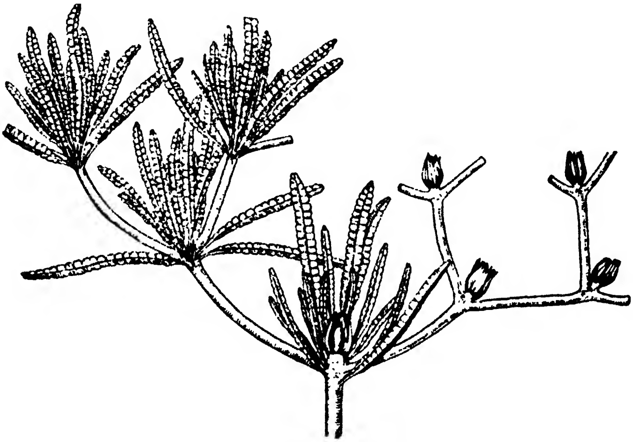


FIG. 974. *Wielandiella angustifolia*, a Mesozoic cycad, with leaves and strobili After Nathorst

Williamsonia. The most important group of Mesozoic cycadophytes is represented by the genus *Williamsonia* (Fig. 972). This genus had leaves resembling those of *Cycadeoidea* and modern cycads; but the stems, in contrast to the greatly enlarged ones of the latter types, were slender, often no more than one to five centimeters in diameter, and frequently they were branched.

In many and possibly all species the seed and stamens were borne separately. The female cone was similar to that of *Cycadeoidea*. It was surrounded by sterile bracts which gave the whole structure the appearance of an artichoke. This was borne at the end of an elongated scaly stalk. In the male "flower" the stamens were in a whorl, without, as far as is known, any covering of bracts. The bases of the stamens were united as in *Cycadeoidea.*

Williamsoniella. The genus *Williamsoniella* had slender branching stems about two centimeters in diameter, and simple leaves (Fig. 973). In a related genus the leaves were pinnately divided (Fig. 974). The strobilus or "flower" was borne on a stalk, and consisted of an ovuliferous cone surrounded by a whorl of stamens (Fig. 975). The stamen was simple, with a prominent ridge on the upper surface; on each side of the ridge were three synangia. The ovuliferous cone was similar to that of *Cycadeoidea.*

In the best-known species, but apparently not in all, the axis of the ovuliferous cone was prolonged into a sterile tip, while the ovules were sessile and not stalked as in *Cycadeoidea.*

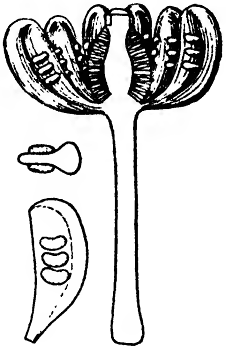


FIG. 975. Longitudinal section of strobilus of *Williamsoniella coronata*

Showing ovulate cone surrounded by staminate sporophylls. Also staminate sporophyll as seen in section and from the side

Order *Cordaitales*

General characteristics. The *Cordaitales* are an order of gymnospermous trees which were very abundant in Carboniferous times and almost entirely disappeared before the close of the Permian. They were tall, slender trees, with branching crowns and clear unbranched trunks ten, twenty, or thirty meters in length (Fig. 976). Some characteristic species had long, narrow leaves reaching lengths, in different species, of from thirty centimeters to a meter (Figs. 977, 978). Others had smaller leaves, more like those of large-leaved species of the modern coniferous genus *Agathis* (Fig. 992). The long-leaved species had what to us would be a most unusual appearance, something like a tree yucca on an elongated trunk. The smaller-leaved kinds must have looked rather modern as compared with the giant lycopods and calamites of their time. The leaves had numerous parallel veins which ran lengthwise and in most cases repeatedly forked dichotomously.

The secondary wood was like that of certain modern conifers, but the pith was wider and so more like that of cycads (Fig. 979).

Reproduction of *Cordaitales.* Pollen and ovules were produced in separate cones (Fig. 977). The male cone consisted of a central axis bearing sterile bracts among which were the stamens (Fig. 980). Each stamen consisted of a slender filament surmounted by three, four, or more long vertical sporangia, or pollen sacs. Among all known plants the stamens of the *Cordaitales* show the greatest resemblance to those of *Ginkgo.* The female cones were similar to

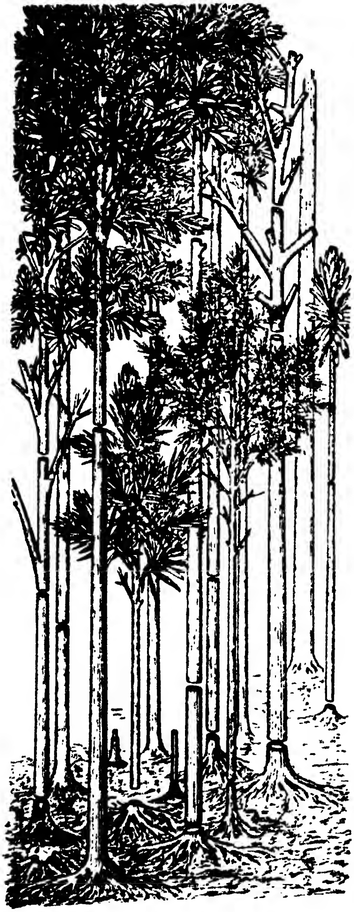


Fig. 976. Various species of *Cordaitales*

After Grand' Eury

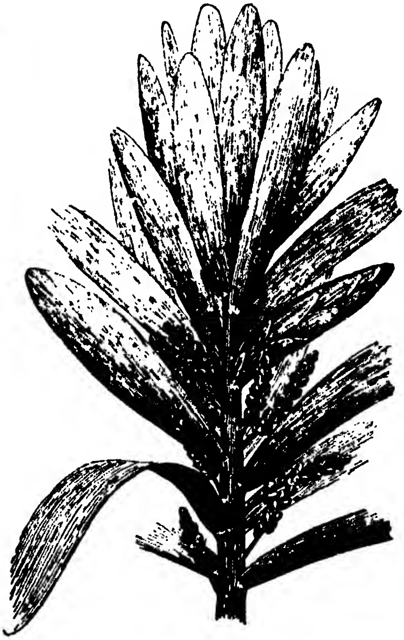


Fig. 977. End of a branch of *Cordaites* with strobili and a young branch

After Grand' Eury

the male. Most of the scales were sterile, while ovules were borne singly on stalks in the axils of some (Fig. 981).

Seed. The seed were like those of the seed-ferns (Fig. 982).

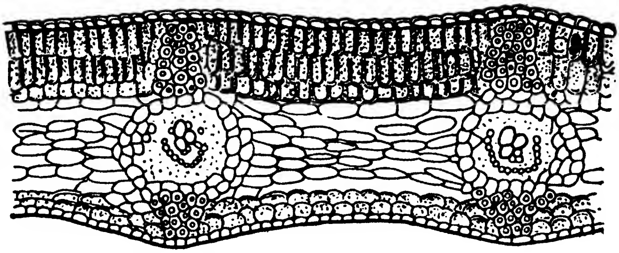


FIG. 978. Cross section of a leaf of *Cordaites*

After Renault

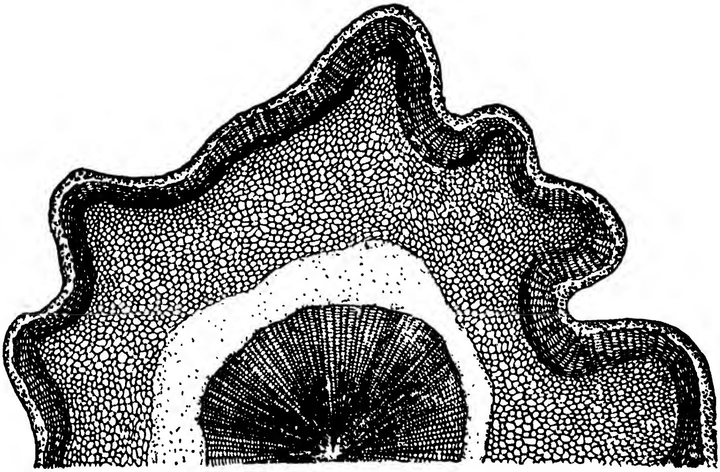


FIG. 979. Cross section of a young stem of *Cordaites*

Note extensive development of secondary xylem. Around the xylem is a poorly preserved region in which the phloem is situated. Exterior to this is the cortex. Note tissue formed by activity of the phellogen layer near the periphery of the stem

The nucellus was surrounded by an integument, and contained a large prothallus which produced archegonia at its apical end. At the apex of the nucellus is a pollen chamber in which pollen grains are found. As in seed-ferns, the pollen grain contained a multicellular structure (Fig. 983), perhaps an antheridium, and grew while within the pollen chamber.

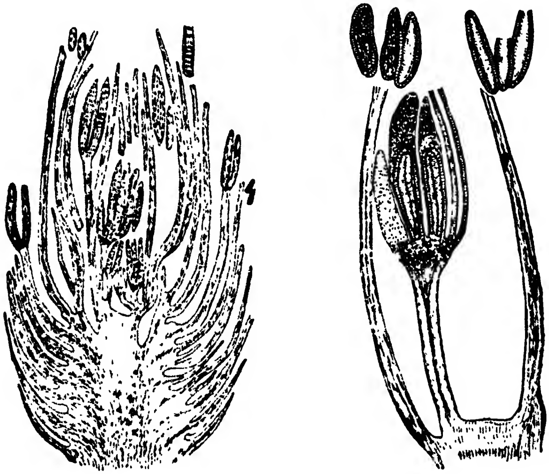


Fig. 980. Stamens of *Cordaitales*

Left, section through staminate strobilus (× 6). Right, section through three stamens (× 20)

Affinities of *Cordaitales*. The stems of typical *Cordaitales* are more like those of conifers than like typical seed-ferns. However, there is a very complete series of intermediate forms which lead from seed-ferns to the *Cordaitales*, thus indicating a relationship between the two groups. This relationship is emphasized by the facts that the seeds of the two groups agree very closely in structure and that the development of the pollen grains is similar. The seed-ferns are more ancient geologically than the *Cordaitales*.

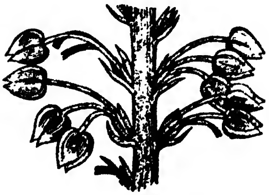


Fig. 981. Seed of *Cordaitales*

After Saporta

In regard to the differences in the external form of the leaves, it must be remembered that this may be a variable feature in a single group of plants, as is seen in modern ferns and flowering plants. That the same may have been true of seed-ferns is indicated by certain large coarse entire leaves which were abundant in the late Paleozoic, and which are believed by most paleobotanists to have been the foliage of seed-ferns.

Altogether, the evidence is not inconsistent with the belief that the *Cordaitales* were descended from seed-fern stock, but that they branched off at an early date.

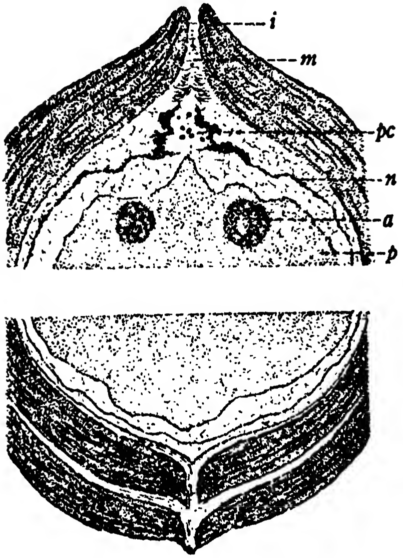


Fig. 982. Longitudinal section of ovule of *Cordaitales*

i, integument; *m*, micropyle; *pc*, pollen chamber; *n*, nucellus; *a*, archegonia; *p*, prothallus. (After Renault)

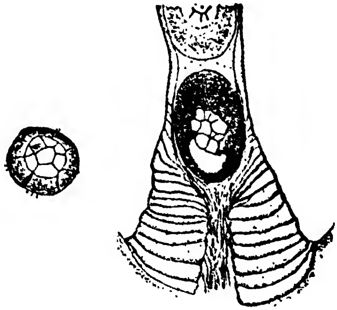


Fig. 983. Pollen grains of *Cordaitales*

Left, section of a micropyle showing pollen grains; right, pollen grain showing cellular structure. (After Renault)

On the other hand, the great similarity in the wood, leaves, and reproduction of the *Cordaitales* and the *Ginkgoales* leaves little doubt that the latter are descended from the former.

Likewise, among the conifers and in the *Cordaitales* we find the same general habit; the same type of wood; striking similarity in leaf structure; and methods of reproduction which have much in common, particularly in the structure of the seed. The facts are consistent with the widely accepted view that the conifers are of cordaitalian stock.

Fig. 984. *Ginkgo biloba*

This is the tree in which Hirase discovered the spermatozoids of *Ginkgo*, the first spermatozoids ever seen in seed plants. (Photograph by Dr. H. H. Bartlett)

Order *Ginkgoales*

General characteristics. The order *Ginkgoales* is represented in our present flora by the single species *Ginkgo biloba* (Fig. 984). In the Mesozoic there were several species. In that era *Ginkgo* and a genus with divided leaves, *Baiera* (Fig. 985), were very common and widespread and were a dominant element in the flora. *Ginkgo* is a fair-sized or large tree, and as far as is known the *Ginkgoales* of the Mesozoic were also trees. They were probably the most numerous trees of the period.

The leaves of *Ginkgo biloba* are fan-shaped and are very often two-lobed. The veins are parallel and branch dichotomously, thus recalling those of ferns or the *Cycadofilicales*. In shape and general appearance the leaf, except for being larger and coarser, is very similar to that of the maidenhair fern, from which resemblance *Ginkgo* gets its name of maidenhair tree.

Ginkgo is almost unknown as a wild plant, and has been reported only by travelers in forested regions in western

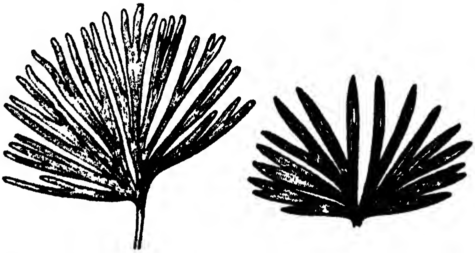


Fig. 985. Leaves of *Baeria munsteriana* and *Baiera gracilis*, Mesozoic *Ginkgoales*

China. For a long time it has been cultivated in China and Japan. *Ginkgo* is now widely cultivated in temperate countries as an ornamental tree. It certainly seems that *Ginkgo* would be nearing extinction had it not been preserved from that fate by cultivation.

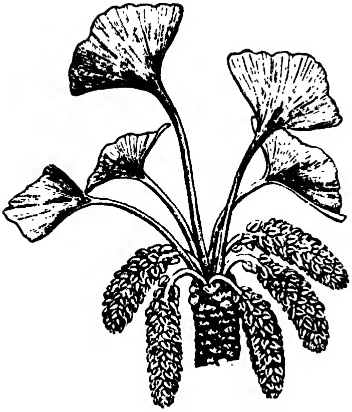


FIG. 936. Branch of *Ginkgo* bearing strobili of male sporophylls. (× ⅓)

Reproduction. *Ginkgo* is dioecious, the stamens and ovules being on separate plants. The staminate strobili are formed in groups at the ends of short branches (Fig. 986). Two or more pollen sacs are borne at the end of each stamen. The ovules are borne in pairs at the ends of slender stalks which occur in groups at the ends of short branches (Fig. 987). The ovule is very similar to that of the cycads. As in the latter, there is a nucleus surrounded by a single integument (Fig. 988). The prothallus is a large oval structure which develops within the nucellus. At the apex of the nucellus there are usually two archegonia. The pollen grain germinates to give rise to a pollen tube as in the cycads; and in the end of the tube there are produced two motile spermatozoids similar to those of the cycads. The seed of *Ginkgo*, including the gametophytes, is thus seen to be very similar in its anatomy and physiology to those of the cycads (Fig. 989).

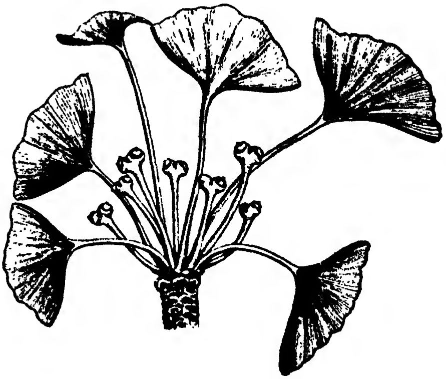


FIG. 987. *Ginkgo biloba*

End of branch bearing young leaves and young ovules. (× ½)

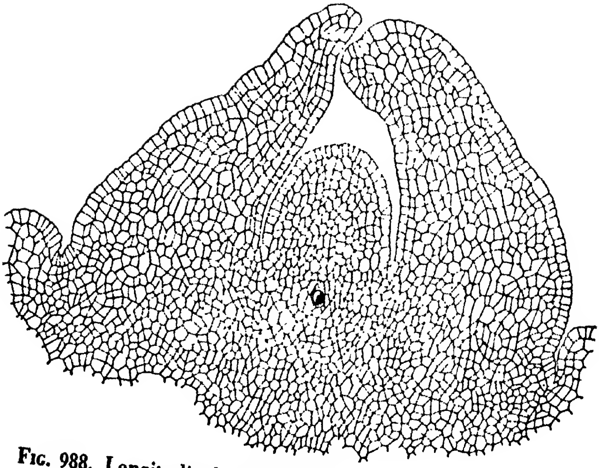


FIG. 988. Longitudinal section through an ovule of *Ginkgo*
Showing nucellus containing a spore mother cell and surrounded by integument.
(× 85)

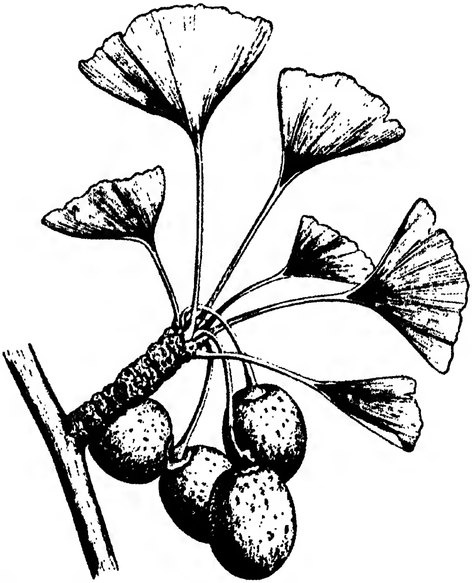
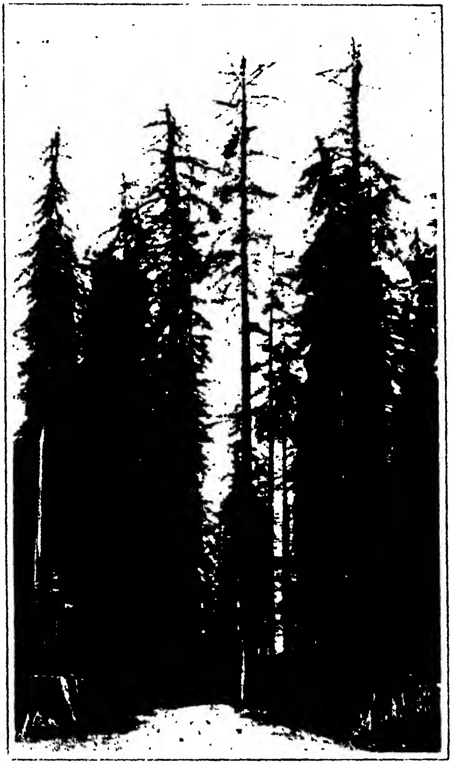


FIG. 989. Branch of *Ginkgo* with seeds which have developed from ovules.
(× ½)

The chief interest in *Ginkgo*, perhaps, lies in its motile spermatozoids. In general habit and anatomy *Ginkgo* is very much like a conifer. In conifers fertilization is due to male nuclei, as in angiosperms, and not to spermatozoids. In *Ginkgo* the spermatozoids are carried by the pollen tube to an archegonium. The presence of flagella on the spermatozoids in such a pronounced land plant can be interpreted only as a survival of structures which originated in aquatic ancestors of *Ginkgo* and were still useful in less distant ancestors when the spermatozoid had to swim from an antheridium to an archegonium.



Photograph by Dr. William S. Cooper

FIG. 990. Three-hundred-foot redwood, Humboldt County, California

Relationship of *Ginkgoales*. The *Ginkgoales* appear to be descended from the *Cordaitales*. The general anatomy and venation of the leaves of *Ginkgo* recall those of the *Cordaitales*. In various respects *Ginkgo* is intermediate between the *Cordaitales* and the *Coniferales*. The staminate strobili of *Ginkgo* are similar to those of the *Cordaitales* except that those of *Ginkgo* lack the large sterile bracts found in the strobili of the *Cordaitales*. The general character of the seed in all three groups is similar. It is probable that in the *Cordaitales* an antheridium developed inside the pollen grain and that spermatozoids were formed in the antheridium. In *Ginkgo* fertilization is still effected by spermatozoids, but these are produced in pollen tubes. In the *Coniferales* there are pollen tubes, but in these spermatozoids have given way to male nuclei as in angiosperms. The stems have a small pith like the conifers and not a wide one as in the *Cordaitales*.

Order *Coniferales*

The conifers are woody plants ranging in size from shrubs to the giant *Sequoia* of California (Fig. 990). Many of them contain numerous resin canals (Fig. 135).

Leaves. The leaves are xerophytic (Fig. 991), are usually small, and in many species are needlelike or scalelike. In a few genera the lamina is rather broad (Fig. 992). The leaves usually remain on the plant for several years, being deciduous in only three genera.

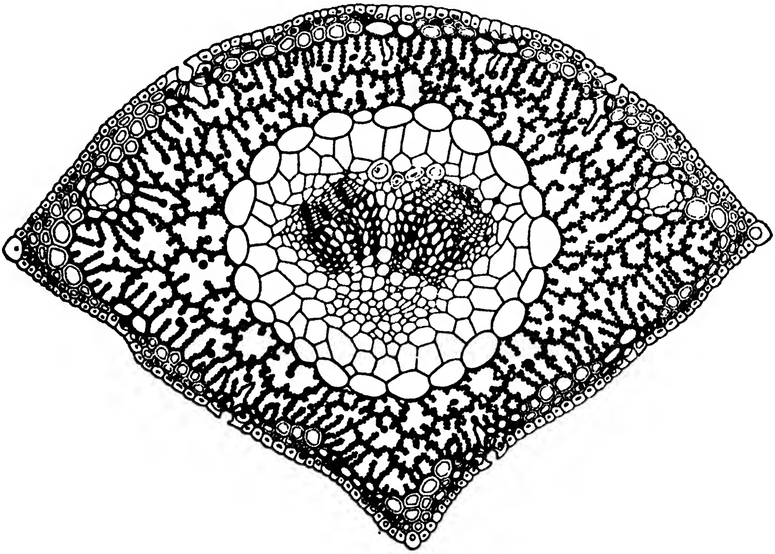


Fig. 991. Cross section of leaf of pine (*Pinus insularis*)

Stem structure. The arrangement of the vascular bundles and of the secondary thickening of the conifers is very similar to that of dicotyledonous angiosperms. There is a small pith surrounded by a wide woody cylinder. The structure of the wood differs from

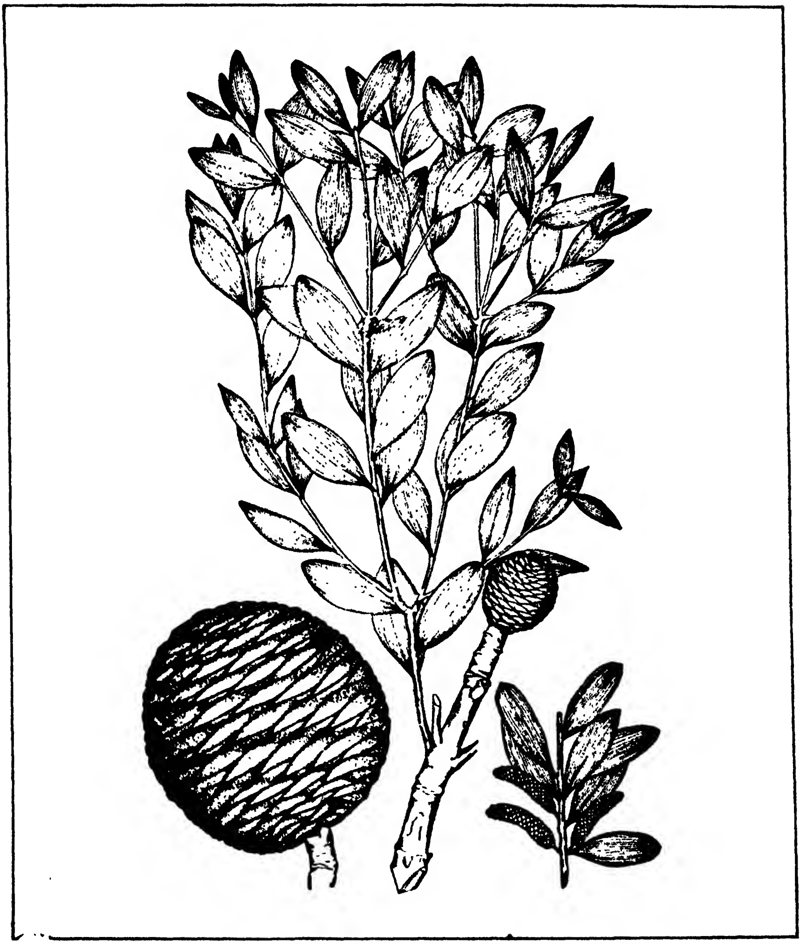


FIG. 992. *Agathis alba*, the source of Manila copal
Lower left, female cone; lower right, small branch with male cones (× ⅓)

that of dicotyledons in that it contains only tracheids and wood parenchyma and lacks vessels and wood fibers (Fig. 146). The tracheids serve both for water conduction and as strengthening elements. Owing to the absence of vessels and wood fibers the wood of the conifers is much more primitive than that of the flowering plants. The xerophytic structure of the leaves is connected with the primitive nature of the wood and the large size of the plants, since tracheids are not as well fitted for conducting large quantities of water as are vessels.

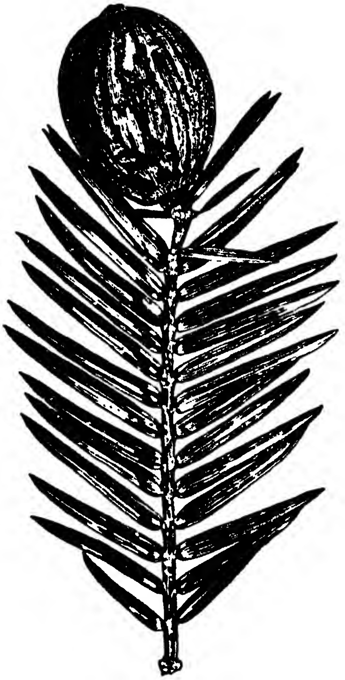


Fig. 993. Mature seed of *Torreya taxifolia*

The fleshy covering which makes it look like a plum is formed by the outer part of the outer integument. (× ¾). After Coulter and Land

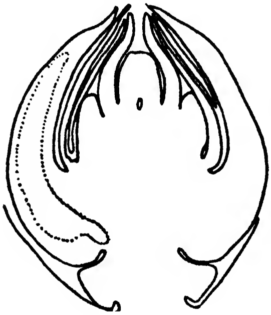


Fig. 994. *Torreya taxifolia*

Longitudinal section of an ovulate strobilus showing bracts, integuments, and nucellus with spore mother cell. (× 20). After Coulter and Land

Sporangia. The pollen sacs are borne in small cones. In the majority of genera the ovules are also in distinct cones, and the seed when ripe is dry. In some genera the cone is so greatly reduced as not to have the appearance of a cone, and produces only a single ovule, and in this case the seed is more or less surrounded by a fleshy covering (Figs. 993, 994).

Pine. The genus *Pinus*, the pines (Fig. 995), are such widely distributed, well-known, and typical conifers that they may be taken as a good example of the order *Coniferales*.

Vegetative structure. The crown has a conical form, owing to the fact that both the central stem and the branches have an excurrent form of growth. The branches are of two kinds, long branches and short branches with limited growth. The only leaves on the long branches are scale leaves, a feature not characteristic of all conifers. The short branches arise in the axils of the scale leaves and bear needle-shaped green leaves, singly or in clusters (Fig. 996). The short branches are deciduous, being shed with the leaves (Fig. 996).

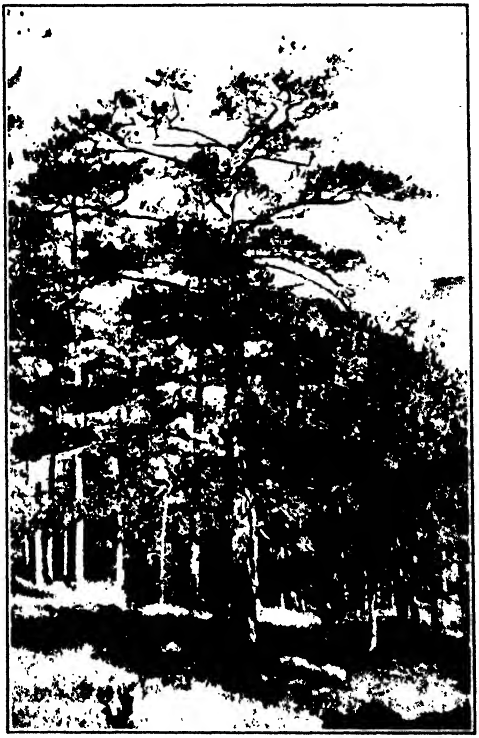


FIG. 995. ***Pinus insularis*** **forming an open forest in the mountain region of Luzon, in the Philippine Islands**

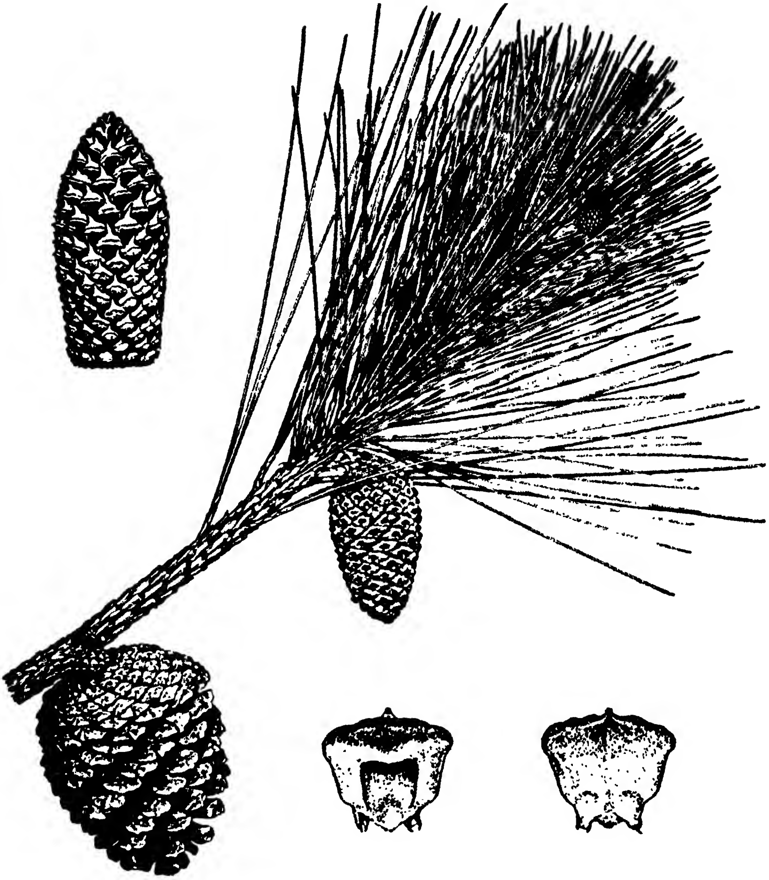


FIG. 996. Pine (*Pinus insularis*)

Center, a branch bearing cones of three different years; the small ones at the tip have recently been pollinated, the next in age is about a year old, while the oldest has opened to shed its seeds (× ⅓). Upper left, a cone at the age of pollination; note that the sporophylls are separated so that the pollen can enter between them (× 3½). Lower right, young scale, first as seen from below, showing bract, and then as seen from above, showing two ovules (× 6)

Ovule and female prothallus. The ovules are produced in cones (Fig. 996). The cones terminate special short branches. Each ovule-bearing component of the cone consists of a bract and above this an ovuliferous scale with two ovules (Fig. 996). This compound structure does not seem to be a simple sporophyll, but there is great difference of opinion as to its morphological nature. The ovuliferous scales are the conspicuous scales in the mature cone. The ovules occur near the base of the ovuliferous scale, and are directed toward the central axis of the cone.

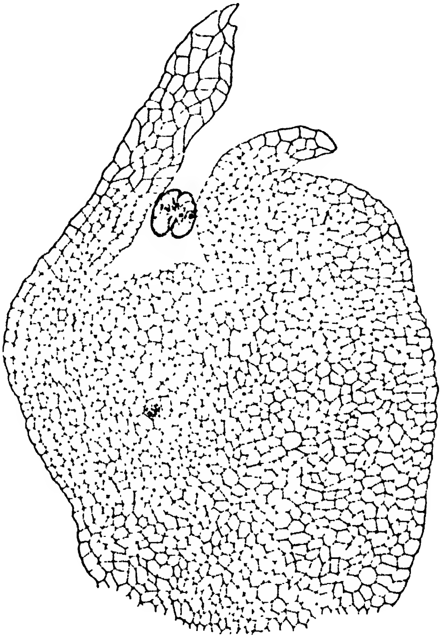


FIG. 997. **Longitudinal section of ovule of pine**

The ovule consists of the nucellus surrounded by an integument. The nucellus is free from the integument only near the apex; within the nucellus is the spore mother cell, the contents of which are shaded. In the opening (micropyle) there are two pollen grains containing male prothalli. (× 100)

The ovule resembles that of the cycads in that it consists of a nucellus surrounded by a single integument (Fig. 997). A spore mother cell is formed within the nucellus and divides to form a row of four spores (Fig. 998). The three apical spores degenerate, while the basal one germinates (Fig. 998) and produces a female prothallus (Fig. 999) which, as in all of the spermatophytes, remains permanently enclosed within the ovule. The female prothallus is a white oval mass, at the apical end of which archegonia are produced. A mature archegonium consists of a large egg cell and the neck cells (Figs. 1000, 1001). At one stage there is an evanescent ventral canal cell (Fig. 1002). A comparison of the cycads and of pine shows that the general structure of the ovules and female prothalli is very similar in the two cases.

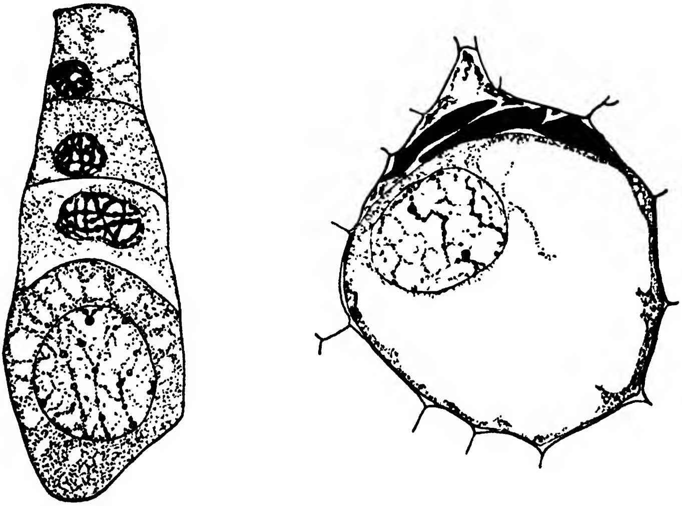


Fig. 998. Gynospores (megaspores) of pine

Left, row of four megaspores of pine; the basal one will give rise to the female prothallus. Right, three apical megaspores are disorganizing, while the basal one has enlarged considerably. (After Ferguson)

As in the cycad, the first divisions of the spore nucleus are not followed by wall formation, and free nuclear division results in a number of nuclei which lie free in the cytoplasm. Also as in the cycads, a large central vacuole appears and presses the cytoplasm with its contained nuclei against the spore wall, where at first the cytoplasm forms a thin peripheral layer (Fig. 1003). Finally cell walls begin to form from the periphery of the prothallus, and this process extends inward until the whole prothallus becomes cellular.

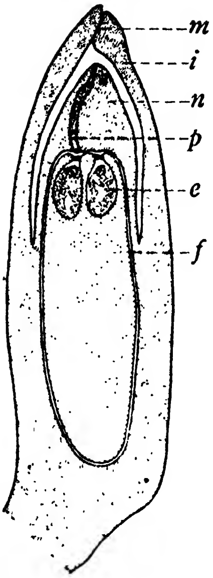


FIG. 999. Somewhat diagrammatic longitudinal section of ovule of pine, containing a female prothallus with two archegonia

m, micropyle; *i*, integument; *n*, nucellus; *p*, pollen tube; *e*, egg in archegonium; *f*, female prothallus. (× 14)

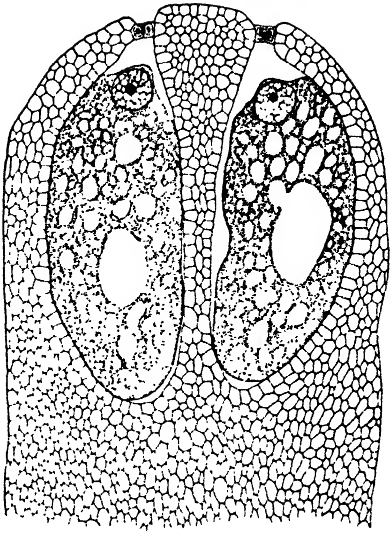


FIG. 1000. Apex of female prothallus of pine, showing two archegonia. (× 75)

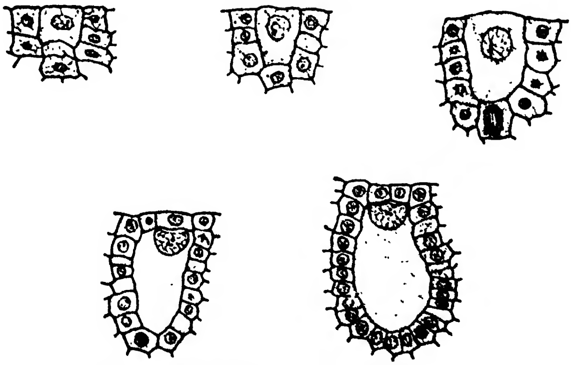


FIG. 1001. Development of archegonium of *Pinus strobus*. (× 115) After Ferguson

Pollen sacs. The pollen-bearing sporophylls are small and are borne in small cones (Fig. 1004). Each has two pollen sacs on its under surface. The male cones occur in clusters near the ends of the long branches, and, like the short branches, are produced in the axils of the scale leaves on the long branches (Fig. 1004).

Pollination. The pollen grains are carried by the wind and deposited in the micropyles of the ovules (Fig. 997). This process is known as pollination. At the time of pollination the female cone stands erect and the scales are spread apart (Fig. 996), so that pollen grains can reach the ovules. After pollination the short stem bearing the female cone bends downward so that the cone hangs vertically, and in this position it remains during the remainder of its existence (Fig. 996).

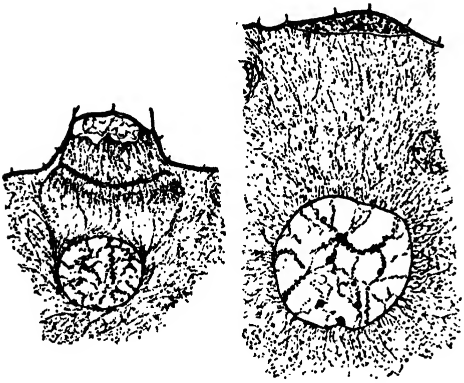


Fig. 1002. Ventral canal cell of *Pinus strobus*

Left, above is seen the ventral canal cell beginning to disintegrate, and below, the egg nucleus. Right, above are the remains of the ventral canal cell, and below, the enlarged egg nucleus. (After Ferguson)

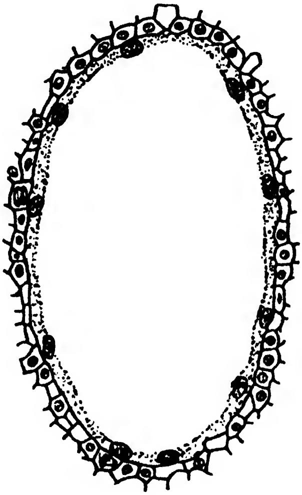


Fig. 1003. Prothallus of *Pinus strobus* in free-nuclear stage. (× 77)

After Ferguson

Male gametophyte and fertilization. The pollen grain (Fig. 1005), before being shed, germinates, and a male gametophyte, or prothallus, is formed within the spore wall. This consists of four cells: a tube cell, a generative cell, and two evanescent prothallial

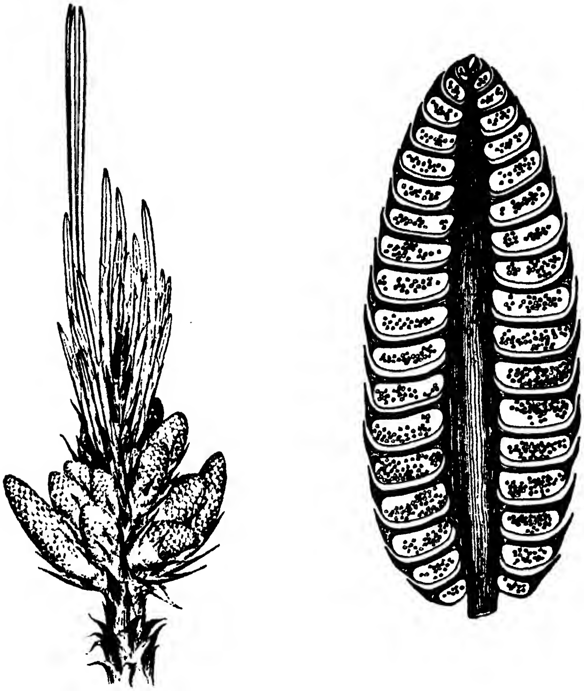


Fig. 1004. Left, branch of *Pinus insularis* bearing male cones (× 1); right, longitudinal section through a male cone (× 5)

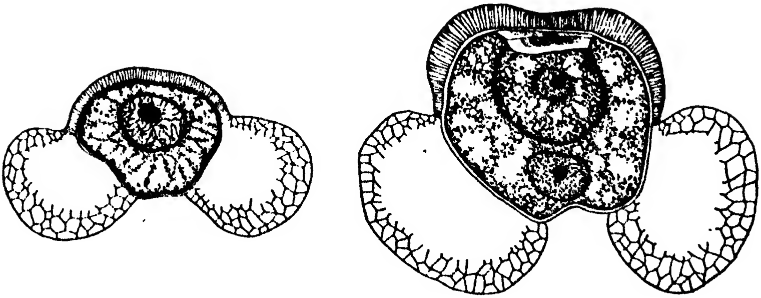


Fig. 1005. Male gametophyte of pine

Left, section of pollen grain of pine; note the inflated wings which make the spore buoyant (× 390). Right, male prothallus within the wall of the microspore of pine; above are two disorganizing prothallial cells; below these is the generative cell; and below and almost surrounding this is the large tube cell (× 530) cells which begin to disorganize as soon as they are formed, so that only remnants of them appear in the pollen grain at the time of shedding. After reaching the micropyle the pollen grain sends out a pollen tube (Fig. 1006) which grows through the nucellus and enters the archegonium. During the growth of the pollen tube the tube nucleus migrates into the tube, and the generative cell divides to form two cells: a stalk cell (toward the degenerating prothallial cells) and a body cell (Fig. 1006). Later the body cell becomes free and passes into the tube, where its nucleus divides to form two male nuclei. Fertilization results from the fusion of one of the male nuclei with an egg nucleus. The most striking differ-

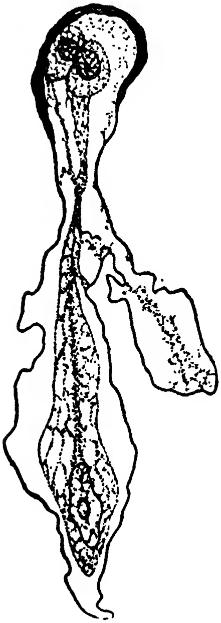


Fig. 1006. Pollen tube of pine

Below, near the apex, is the tube nucleus. Above, and still within the spore wall, are the stalk cell next to the spore wall and, adjoining this, the body cell. (Redrawn after Ferguson)

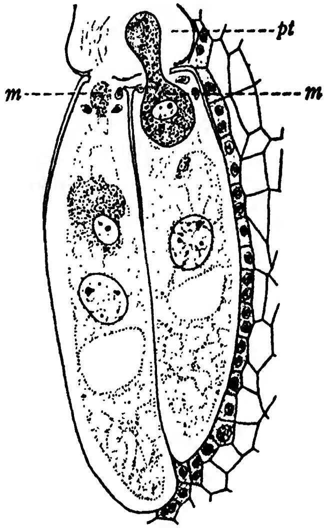


Fig. 1007. Section through two archegonia of *Juniperus communis*

Into each a male cell is entering from the tip of a pollen tube, *pt*. The male cell, *m*, to the right is cut lengthwise and shows plainly. Only a small slice of the male cell on the left is seen in the section. (× 190). After Nichols ence between the sexual method of reproduction in the conifers and that in the cycads and *Ginkgo* is that in the conifers there are no flagellated spermatozoids. The presence of flagellated spermatozoids is a character, derived from aquatic ancestors, which has persisted throughout the divisions *Bryophyta* and *Pteridophyta*, and which among the *Gymnospermae* is still found in the *Cycadales* and *Ginkgo*, but which has disappeared in the *Coniferales* and in all the higher orders of the *Spermatophyta*.

Seed. The fertilized egg germinates and produces an embryo which remains embedded in the prothallus until the germination of the seed. The embryo is a cylindrical structure with a number of cotyledons. The integument forms the seed coat (Fig. 1008).

In pine, as in other conifers, the formation of the embryo is a rather complicated process. The nucleus of the fertilized egg divides to form four nuclei without the formation of cross walls (Fig. 1009). This is the beginning of the proembryo stage. The four nuclei migrate to the base of the archegonium, where they divide to form four tiers of four cells each (Figs. 1009, 1010). This completes the formation of the proembryo. The uppermost tier is not separated by walls from the main cavity of the archegonium, and the nuclei disintegrate. The four cells of the lowest tier form four embryos. The cells just above these are known as suspensors (Fig. 1011 *A*); these elongate greatly and push the embryo farther into the prothallus (Fig. 1011 *B*). This pushing of the embryo into the prothallus is preceded by digestion of the cells of the prothallus, a process which appears to be due to enzymes secreted by the embryos. Each embryo cell first forms a row of cells the lowest of which becomes the true embryo, while the others add to the length of the suspensor (Fig. 1011 *B*, *C*). Finally one embryo grows more rapidly than the others and becomes the single embryo of the mature seed (Fig. 1011 *C*–*K*); the other embryos degenerate (Fig. 1008).

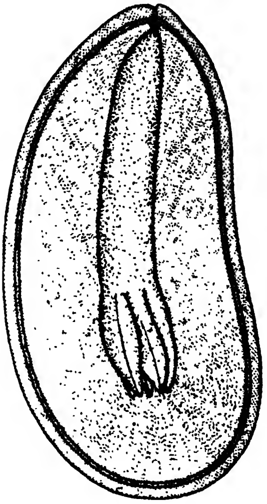


Fig. 1008. Longitudinal section of pine seed

This consists of the embryo surrounded by the female prothallus and this in turn by the seed coat formed from the integument. (× 5)

Alternation of generations. In the conifers the alternation o generations is very similar to that described for the cycads. The sporophyte is a large plant which produces ovules and pollen grains. A spore within the ovule gives rise to a female gametophyte, or prothallus, bearing archegonia, while the pollen grain produces a male gametophyte. The fertilization of the egg in the archegonium results in the production of a sporophyte. There is thus, as in the *Bryophyta* and the *Pteridophyta*, an alternation of a sporophytic and a gametophytic generation. As in bryophytes, pteridophytes, and cycads, the sporophyte is characterized by a double number of chromosomes, reduction taking place during the division of the spore mother cells. The gametophytes have the single number of chromosomes, the double number being restored at fertilization.

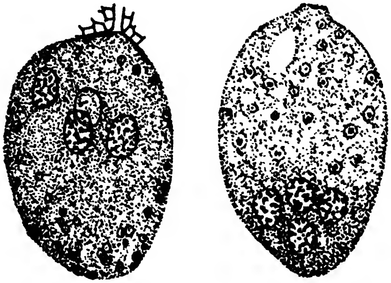


Fig. 1009. Young proembryo of *Pinus strobus*

Left, four nuclei in the position in which they are formed; right, after migration to the base of the proembryo. (After Ferguson)

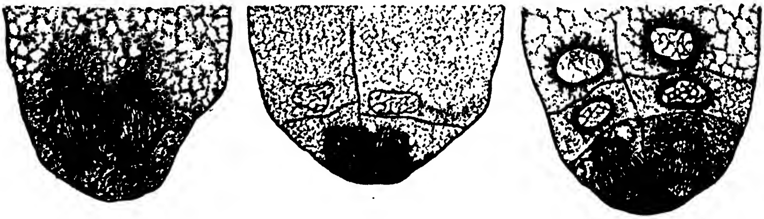


Fig. 1010. Development of the proembryo of *Pinus laricio*

Left, the four nuclei are dividing to form two tiers of cells (only two of the spindles are shown in this picture); center, two tiers of cells have been formed and the nuclei of the lowest tier are dividing (only two of the four cells of each tier are shown); right, three tiers of cells have been formed and the nuclei of the lowest tier have already divided (only two of the four cells of each tier are shown). (× 215). After Kildahl

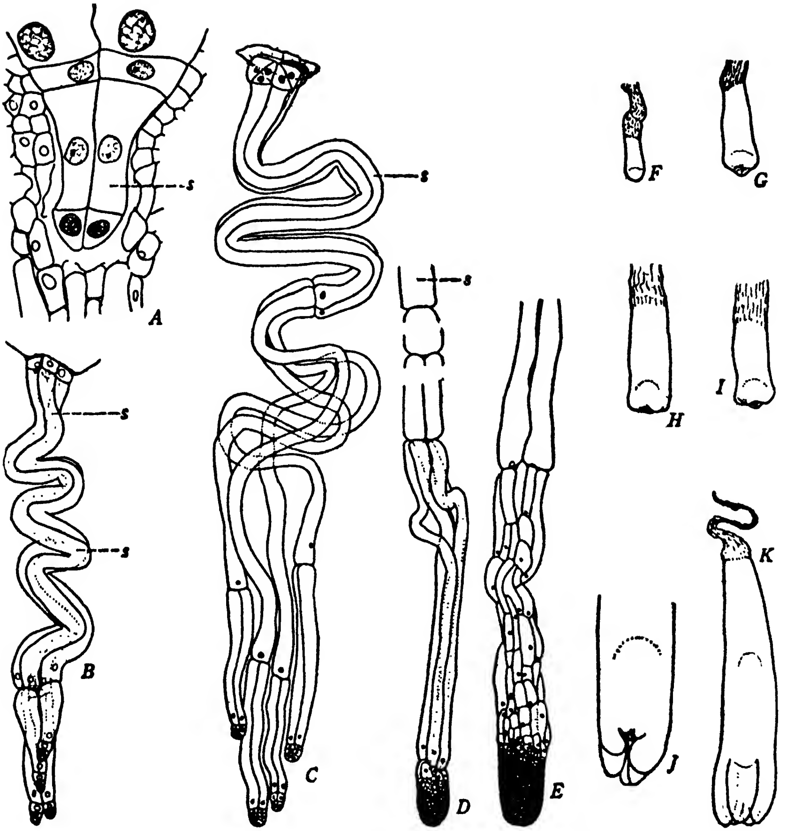


FIG. 1011. Development of embryo of *Pinus banksiana*

A, the suspensors (*s*) of the four-tiered stage have begun to elongate; the embryos are below the suspensors. *B*, later stage in which the suspensors (*s*) have elongated greatly, while the embryo has formed secondary suspensor cells. *C*, still later stage showing further development of secondary suspensors. *D*, further development of embryo; the end of the original suspensor cell is shown at *s*; most of the length of the secondary suspensor cells is omitted. *E*, still later stage in development of embryo. *F–K*, growth of embryo and formation of cotyledons. (*A*, × 176; *B–E*, × 45; *F–K*, × 13). After Bucholtz

Relationship. The *Coniferales* appear to be descended from the *Cordaitales*, which either were derived from the *Cycadofilicales* or were closely related to them. As the *Cycadofilicales* gave rise to the *Cycadales*, the *Coniferales* are related through the *Cycadofilicales* to the *Cycadales*. The *Cycadales*, as we have already seen, are much more primitive than the *Coniferales*. A diagrammatic representation of the relationships of these orders is shown in Fig. 1037.

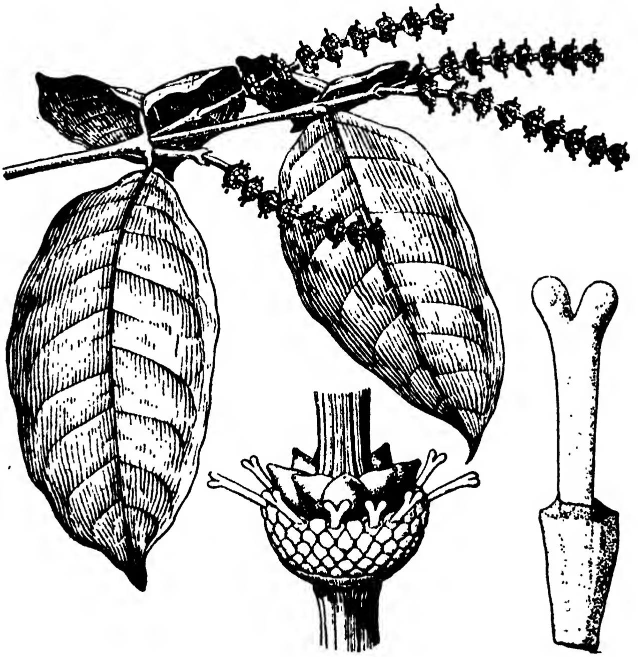


Fig. 1012. *Gnetum gnemon*

Above, habit of plant with male strobili (× ½). Lower left, male strobilus enlarged (× 3). Above the stamens is a circle of ovules, which are usually infertile. Below the ovules is a row of stamens most of which have expanded through the "perianths." Below this row are numerous stamens enclosed in the "perianths." These will expand successively from above. Right, an expanded stamen the base of which is surrounded by the "perianth" (× 12)

Distribution. There is a striking difference between the distribution of cycads and that of conifers. The former are tropical and subtropical, while the latter are found largely in temperate zones. They are particularly characteristic of north-temperate regions, where they form valuable forests of great extent. Conifers are frequently numerous on tropical mountains, and in limited areas may be the dominant element of the flora there.

Order *Gnetales*

General characteristics. The order *Gnetales* is composed of three very peculiar and very dissimilar genera: *Gnetum*, *Ephedra*, and *Welwitschia*. The species of *Gnetum* are either small trees or woody vines found in the tropics (Figs. 1012, 1013). *Gnetum* has fair-sized opposite leaves with netted veins, and in general appearance is similar to a dicotyledonous plant. Species of *Ephedra* are small shrubby plants with opposite scalelike leaves, and in general appearance look something like a much-branched *Equisetum* (Fig. 1014). *Welwitschia*, with a single species found in deserts of southwest Africa, is the most peculiar of all (Fig. 1015). It has a large tap-root, while above ground is a large crown of tissue. Between the crown and the root there are attached two long opposite leaves, which are the only leaves other than the two cotyledons that the plant produces. They grow continually at the base and last throughout the life of the plant.

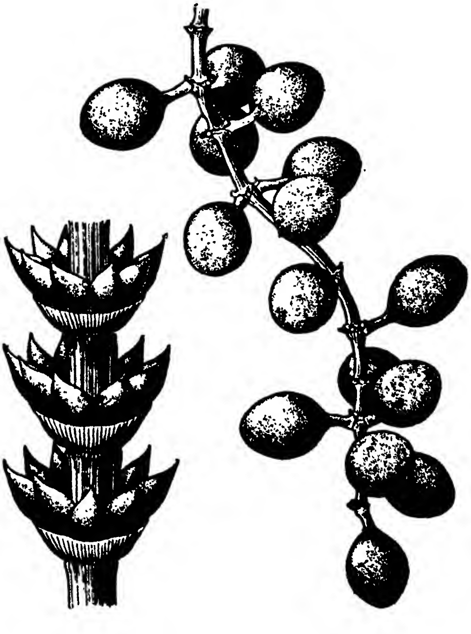


Fig. 1013. *Gnetum indicum*

Left, arrangement of ovules (× 2½). Right, seed (× ⅖)

The *Gnetales* are obviously gymnosperms, as the seeds are not enclosed in ovaries. They have, however, some characters which have been interpreted as showing a similarity to the angiosperms. Among these are the occurrence of vessels in the wood, the presence around the "flowers" of structures which have been considered as similar to the perianth of angio-

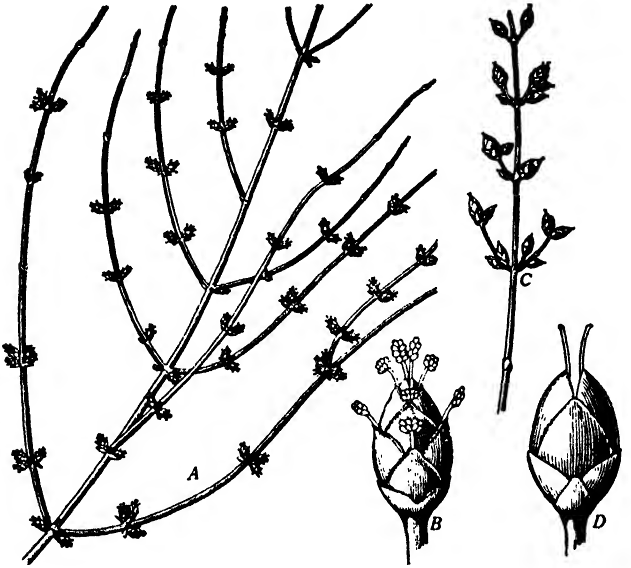


Fig. 1014. ***Ephedra***

A, portion of staminate plant of *E. gerardiana* (× ½); *B*, staminate strobilus (× 4); *C*, ovulate plant of *E. helvetica* (× ½); *D*, ovulate strobilus (× 3)

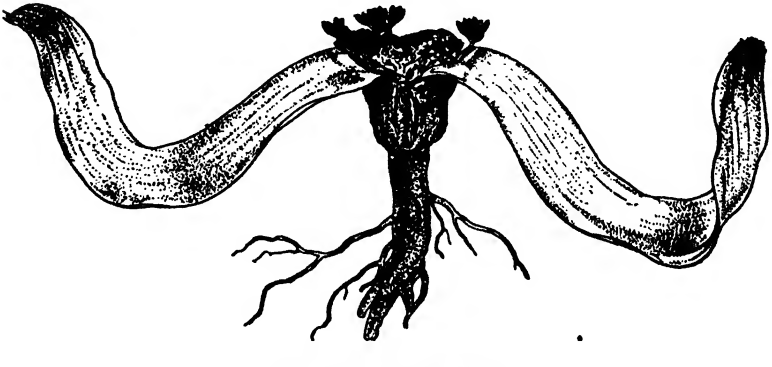


Fig. 1015. ***Welwitschia***

After Hooker

sperms, and the absence of archegonia in *Gnetum* and *Welwitschia.* It has been found, however, that the vessels are formed in a very different manner in *Gnetales* and in angiosperms. The so-called "perianth" in *Gnetales* (Figs. 1012, 1016) is at least as similar to bracts found in some of the gymnosperms as to the perianth of angiosperms. The female gametophyte of *Gnetum* is most like that of the angiosperms, but the nuclei are free in the cytoplasm instead of there being a regular arrangement of cells as in angiosperms (Fig. 1017). The great differences between the three genera indicate a long line of evolution, but unfortunately we know little of the fossil history of the group. The present tendency seems to be to regard the *Gnetales* as representatives of a line of gymnospermous evolution which has not been closely connected with that of the angiosperms.

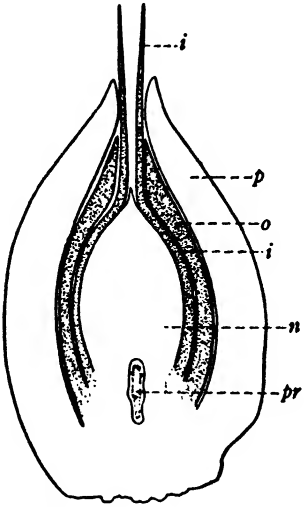


FIG. 1016. Ovule of *Gnetum gnemon*

The integuments are shaded to make them stand out clearly. *p*, perianth; *o*, outer integument; *i*, inner integument; *n*, nucellus; *pr*, prothallus. (Modified after Lotsy)

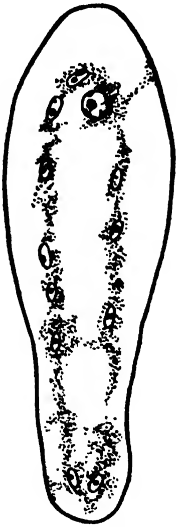


FIG. 1017. Multinucleate prothallus of *Gnetum gnemon*, probably at fertilization stage

After Coulter

CLASS *ANGIOSPERMAE*

The angiosperms are the culmination of the evolutionary process in plants. In them the sporophyte has reached its greatest specialization, while the gametophyte has become greatly reduced. They are the dominant element of our land flora, and in number of species exceed all other green plants. They include all the woody plants other than the gymnosperms and the tree ferns, and all herbaceous plants other than the ferns and fern allies. Many of the angiosperms have become specialized for aquatic conditions, and such species form the dominant vegetation of fresh waters. Angiosperms have also invaded salt water, and even here grasslike forms may be the dominant element of the vegetation in rather quiet water where the bottom is muddy.

The angiosperms are divided into two subclasses, the *Dicotyledoneae* (dicotyledons) and *Monocotyledoneae* (monocotyledons). The distinctive characters of these groups have been given in earlier chapters. The most primitive dicotyledons appear to have been woody; it is believed that the herbaceous dicotyledons and the monocotyledons have been derived from woody dicotyledons.

Sporophyte. The sporophyte is a complicated plant with roots, one or more stems, leaves, and strobili known as flowers.

The wood is highly specialized in that rows of tracheids have become transformed into vessels, while other tracheids are specialized as wood fibers. The vessels are greatly superior to tracheids for the conduction of water, and in most angiosperms the function of the tracheids is largely that of mechanical support. The development of an efficient water-conducting system composed of vessels has enabled angiosperms to produce a great display of mesophytic foliage. The improvement in the conducting system has therefore resulted in a great development of the assimilating system.

Another great advance shown by angiosperms is the development of complicated structures which facilitate insect pollination.

Flowers. The distinguishing characteristic of angiosperms is that the seeds are enclosed in carpels. In some cases there is only one carpel, the edges of which are joined to form an ovary with a single cavity. In many cases one or more carpels unite to form a compound ovary, which may have one cavity or more than one. Where two or more carpels fuse to form a compound ovary, the tips may form separate stigmas or only a single stigma. According to the most generally accepted theory, a carpel is a sporophyll the tip of which has been modified as a stigma.

These carpels and stamens are borne in flowers, and in complete flowers are surrounded by two sets of modified leaves, the petals and the sepals. The torus is a short stem, and as it bears sporophylls the flower is a modified strobilus.

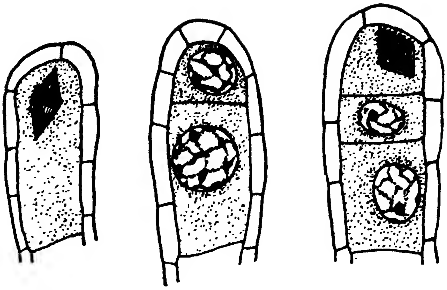


Fig. 1018. Spore mother cell and megaspores of an orchid

Left, spore within nucellus; center, the spore is divided into two daughter cells; right, the lower daughter cell has divided into two spores, while the upper one is in process of division. (After Brown and Sharp)

Ovule and female gametophyte. In the angiosperms the ovule consists of an oval structure, the nucellus, or sporangium proper, surrounded by one or two integuments. At the apex there is a small opening, the micropyle, which extends through the integuments (Fig. 325).

In the nucleus there is usually found a single spore mother cell (Fig. 1018), which in the majority of cases divides to form a

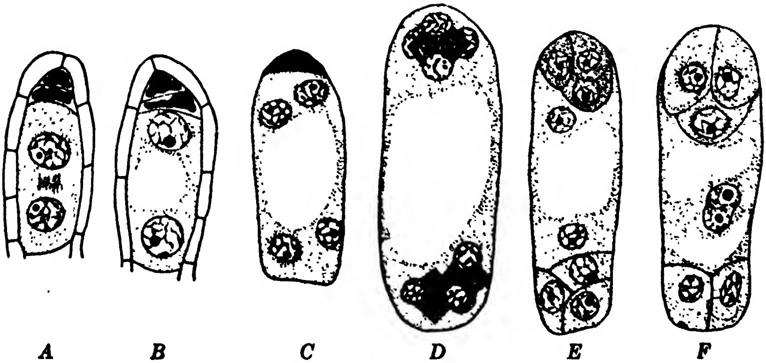


Fig. 1019. Development of female prothallus in an orchid

A, the apical spores are disorganizing; the basal megaspore has enlarged and its nucleus has divided to form two nuclei. *B*, older stage, showing formation of vacuole. *C*, the nucleus at each end has divided, resulting in four nuclei in the prothallus. *D*, telophase of division of four nuclei to form eight. *E*, six nuclei cut off by walls; in the base there are three antipodal cells; at the tip are a large egg cell and two smaller synergids; between the groups of cells are two free polar nuclei. *F*, fusion of the polar nuclei. (After Brown and Sharp) row of four spores (Fig. 1018). The three spores situated toward the apex of the nucellus degenerate (Fig. 1019). The basal spore is also known as the embryo sac, and within it the female gametophyte, or prothallus, is formed. First the embryo sac increases considerably in size and becomes oval in outline (Fig. 1019). Its nucleus divides, and the two daughter nuclei migrate to the opposite ends of the sac. By two successive divisions each of these daughter nuclei gives rise to a group of four nuclei, the groups being at opposite ends of the sac (Fig. 1019). At each end three of the nuclei become surrounded by cell walls. The three cells thus formed at the end of the sac away from the micropyle are known as antipodal cells. The group of three cells at the micropylar end consists of two cells (synergids) and an egg cell. The two nuclei which are free in the cytoplasm are polar nuclei, and they move to the center of the sac. In this condition the female gametophyte is mature and the egg is ready for fertilization.

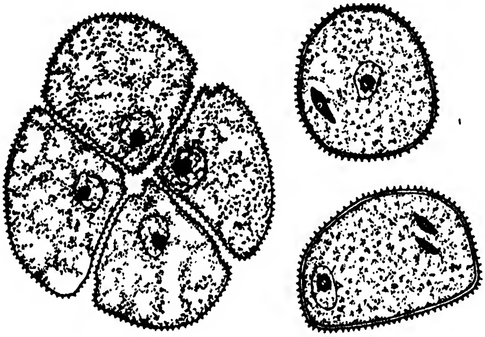


Fig. 1020. Formation of male gametophyte in an angiosperm

Left, a tetrad of pollen grains of an angiosperm (*Elodea*) (× 550); upper right, the microspore nucleus has divided, resulting in the formation of a large tube cell and a small generative cell, which in the figure is situated in the lower left portion of the tube cell; lower right, the generative cell has divided to form two male cells (× 205)

In a considerable number of species the spore mother cell, instead of forming a row of separate spores, becomes the embryo sac.

Male gametophyte and fertilization. The pollen grain begins to germinate before it is shed, and forms a male gametophyte, or prothallus, within the pollen grain (Fig. 1020). This gametophyte is produced by the division of the nucleus of the pollen grain to form a tube nucleus and a generative nucleus. The growth of the pollen tube appears to be connected with the activity of the tube nucleus. The generative nucleus divides to form two male nuclei. This division usually takes place in the pollen tube, but may occur while the pollen is in the anther (Fig. 1020). After being deposited on the stigma the pollen grain sends out a pollen tube into which the nuclei migrate. The pollen tube grows down through the style and enters the female prothallus, usually by way of the micropyle (Fig. 326). The two male nuclei are discharged in the embryo sac. One of them fertilizes the egg by fusing with its nucleus (Figs. 328, 1021). The fertilized egg germinates and produces an embryo. The second male nucleus and the two polar nuclei fuse to form an endosperm nucleus (Figs. 328, 1021).

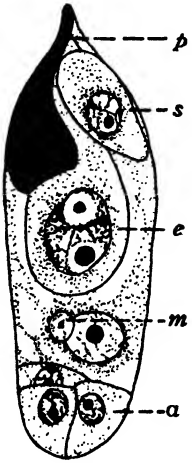


Fig. 1021. Fertilization stage in the embryo sac of an orchid

p, pollen tube; *s*, synergid; *e*, egg containing nucleus formed by the fusion of male and female nuclei; *m*, male nucleus in contact with nucleus formed by the fusion of two polar nuclei; *a*, antipodal cells. (Redrawn after Brown and Sharp)

Endosperm. The endosperm nucleus undergoes a series of rapid divisions which result in the formation of endosperm tissue around the developing embryo, filling the embryo sac. The nuclei of the cells of this tissue contain a triple, or $3x$, number of chromosomes, because the primary endosperm nucleus was formed by the fusion of three nuclei. The endosperm furnishes nourishment for the developing embryo. Usually it completely absorbs the nucellus before the seed is mature. Frequently the embryo absorbs all of the endosperm during the development of the seed; in such cases there is no endosperm in the ripe seed (Fig. 359). In many cases the endosperm persists in the mature seed and is absorbed only during germination (Fig. 360).

Seed. When the endosperm is absorbed during the development of the seed, the ripe seed consists of an embryo surrounded by one or two integuments which form the seed coats. If the endosperm persists in the seed, the embryo is surrounded by the endosperm, and this by the seed coats.

OLDEST ANGIOSPERMS

Caytoniales. In Jurassic rocks have been found the oldest known plants which were angiospermous in the true sense of the term; that is, in having seed enclosed in a carpel. These plants represent two closely-related genera of the order *Caytoniales*.

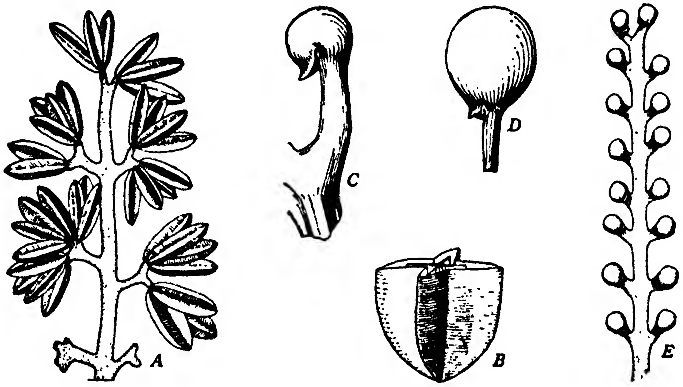


Fig. 1022. *Gristhorpia nathorsti*

A, sporophyll with anthers (× 2); *B*, cross section of anthers showing four locules (× 8); *C*, very young carpel (× 8); *D*, seed (× 4); *E*, sporophyll with carpels (× 1). After Thomas

The carpels were borne on sporophylls. Each sporophyll consisted of a central stalk with pinnately arranged short side branches each of which was terminated by a carpel or fruit. The carpel was completely closed, and the tip of the portion of the pinnule which bent over became the stigma. Pollen grains have been found attached to the stigmas. The seed were borne within the closed carpel (Fig. 1023). The integument of the seed is rather strikingly similar to that of certain seed of seed-ferns. The fruits were fleshy, so the seeds may have been scattered by animals that ate the fruit.

The anthers are found on sporophylls similar in general outline to those which bore the carpels. The branches of the sporophylls divided, and the tips of the divisions bore groups of stamens (Fig. 1022). The anthers were sessile or at the ends of short filaments. They had a four-winged form, and each wing seems to have contained a pollen sac. Thus they had the same general form as the stamen of a modern angiosperm.

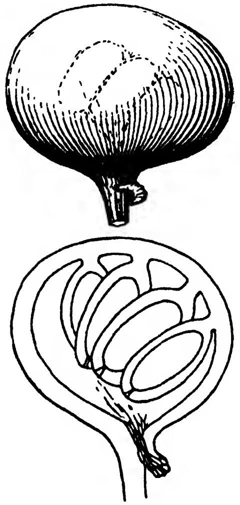


Fig. 1023. ***Caytonia sewardi***

Above, fruit with flange-like stigma on the stalk (× 4.7). Below, diagrammatic section of a fruit to show arrangement of the seeds. (After Thomas)

The leaves which appear to belong to the known *Caytoniales* are of a type which was very widespread during the Jurassic period and extended from Triassic to Cretaceous times. The venation was netted, but similar to that of *Glossopteris*, which is generally regarded as a seed-fern.

The general character of the leaves, sporophylls, and seed indicate that the *Caytoniales* were derived from the seed-ferns.

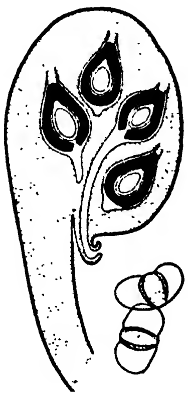


Fig. 1024. ***Caytonia thomasi***

Left, longitudinal section of fruit showing seed. In one case the canal leading to a seed is shown. Right, pollen grains. (After Harris)

In the *Caytoniales* from the Jurassic the pollen seems to have been caught on a stigma, and the ovules are enclosed in ovaries, but in a form from the upper Triassic pollen grains are found in the micropyles of the seed. In this form there appear to have been canals running through the "stigma," and through these canals pollen grains reached the micropyles of the seed (Fig. 1024). This Triassic *Caytonia* is evidently not yet completely angiospermous. It has been suggested that the walls of the fruit of the *Caytoniales* had their origin in the fusion of cupules which surrounded the seed of *Cycadofilicales*.

Unfortunately we do not know how the sporophylls of the *Caytoniales* were borne, or what kind of plant bore them, and so the relationship of the *Caytoniales* to modern angiosperms is obscure.

ANCESTRY OF ANGIOSPERMS

The ancestry of angiosperms has long been a moot question. There is not enough evidence to reach a definite decision, and there is much disagreement as to theory.

Among living gymnosperms the group which is most similar to the angiosperms is the *Gnetales*. While there is great dissimilarity between the *Gnetales* and the angiosperms, still there is enough similarity to convince many that either the angiosperms are descended from the *Gnetales*, perhaps from extinct forms, or else the two groups are closely related and have a common ancestry. Some regard the *Gnetales* as being intermediate between the conifers and angiosperms, and so are inclined to a belief in a coniferous ancestry for angiosperms. This belief is based in part on similarity in wood structure and on the fact that in conifers, *Gnetales*, and angiosperms the fertilization is by male nuclei and not by spermatozoids as in all other living groups of land plants.

A rather complete understanding of the "flower" of *Cycadeoidea* was followed by an extensive discussion of a cycadophyte ancestry for angiosperms; not from *Cycadeoidea* with its highly specialized stem, rather from one more nearly related to *Williamsonia* or *Williamsoniella*, but still more primitive. It was pointed out that, as previously mentioned, the bracts, stamens, and ovuliferous cone of *Cycadeoidea* were in the same relative positions as the perianth, stamens, and carpels of the angiosperms. Also, the embryo had two cotyledons, while the seeds were almost enclosed by the interseminal bracts.

The discovery of the *Caytoniales*, first in the Jurassic and later in the late Triassic, has been taken by some as indicating that the angiosperms, through forms related to the *Caytoniales*, are descended direct from the seed-ferns. A recent theory is that the carpels of angiosperms were derived through a modification and fusion of cupules which surrounded the seeds of *Cycadofilicales*, and that the ovaries of the *Caytoniales* represent an intermediate condition between the seed-ferns and modern angiosperms.

One feature which is common to practically all theories as to the origin of the angiosperms is that they go far back into early Mesozoic or latter Paleozoic times; also that their ancestors were generalized forms and not such specialized ones as modern conifers or cycads or the late Mesozoic cycadeoideas. A conservative suggestion is that they were derived from somewhere in the general gymnospermous complex, from a line in which the marked peculiarities of more modern groups had not become so pronounced as they appear in the well-known specialized types.

Our ignorance as to the ancestry of the angiosperms is not surprising when we remember how scanty is our knowledge of plant floras. If, as seems probable, the angiosperms evolved in Arctic regions, much of the record may be thickly covered with an icy mantle and inaccessible to us. Also, the record of former vegetation is largely that in and around swamps, about lakes, and in similar situations; and any trace of much of that which flourished on higher ground is forever lost. However, in comparatively recent years a great deal of evidence as to the history and relationships of land plants has been discovered; so we may hope that perhaps some day we may have a fairly connected account of the development of the angiosperms.

CHAPTER XXIX

PALEOBOTANY

Introduction. In a previous chapter we discussed the methods by which great masses of sedimentary rocks have been formed, how fossils have been preserved, and the division of geological time into eras and periods. In preceding chapters we have studied the structure and relationships of plants appearing in various geological periods. In this chapter we will consider the successions of floras from the beginning of the geological record to the present, and in this way bring together the long history of the development of plants in a more or less connected story.

PRE-CAMBRIAN PLANTS

Early development of plants. The length of geological time before the dawn of the Paleozoic at the beginning of the Cambrian far exceeds that of all subsequent times. We have very little knowledge of what actually took place during these long ages, but it must have been a period in which the algae were developing, as algal remains indicate that all the great groups of algae had representatives along the shores of the early Cambrian seas. In the chapter on bacteria we noted that there is evidence for the presence of bacteria in the Archeozoic, the earliest of geological eras, and that their presence in this ancient time is in harmony with the view that the bacteria are not only the simplest but also the most primitive of living plants. In the Proterozoic, the succeeding era, bacteria and blue-green algae appear to have been widespread. Evidence for the presence of blue-green algae is given in the chapter dealing with these forms.

LOWER PALEOZOIC PLANTS

The age of algae. The lower Paleozoic has been called the age of algae because, beginning with the Cambrian, a considerable variety of fossils of algae are known (Fig. 1025). No land plants have been found in strata earlier than the Devonian. It is not improbable that land plants did occur in the Silurian; but, if so, they were probably very primitive forms. Most algae are very soft and do not make very good fossils. In general the fossil shows only the external form of the plant. It is therefore rather difficult

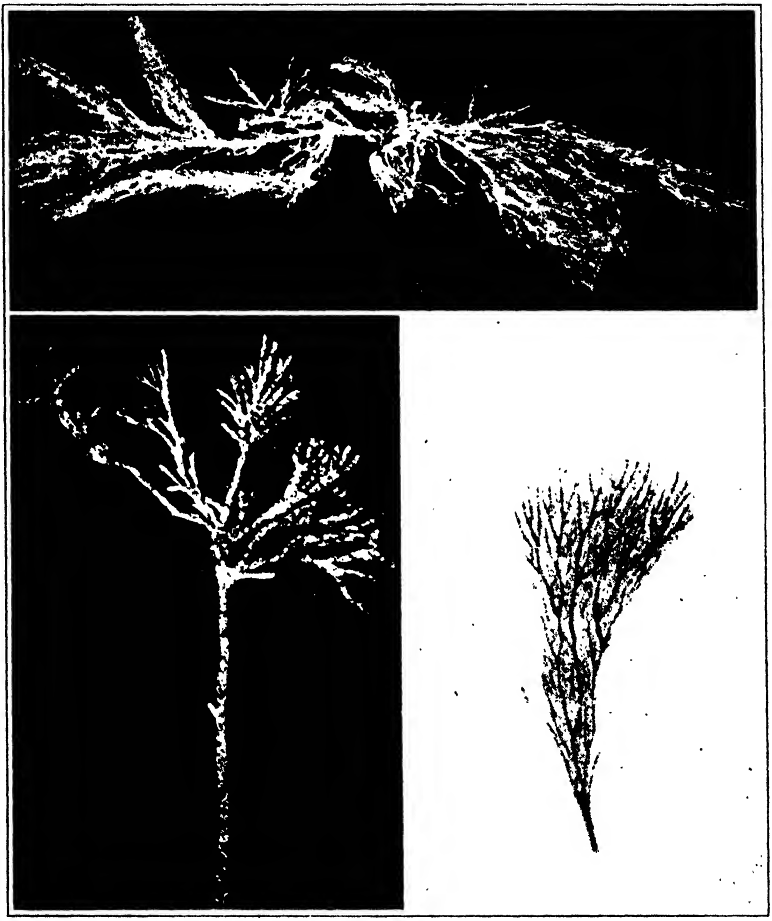


Fig. 1025. Cambrian algae

Above, *Marpolia spirra*; lower left, *Dalyia racemata*; lower right, *Wahpia mimica*. All slightly less than twice natural size. (After Walcott) to decide definitely to what groups fossil algae belong. The forms of Cambrian algae indicate, however, that a variety of blue-green, green, brown, and red algae were present at that time.

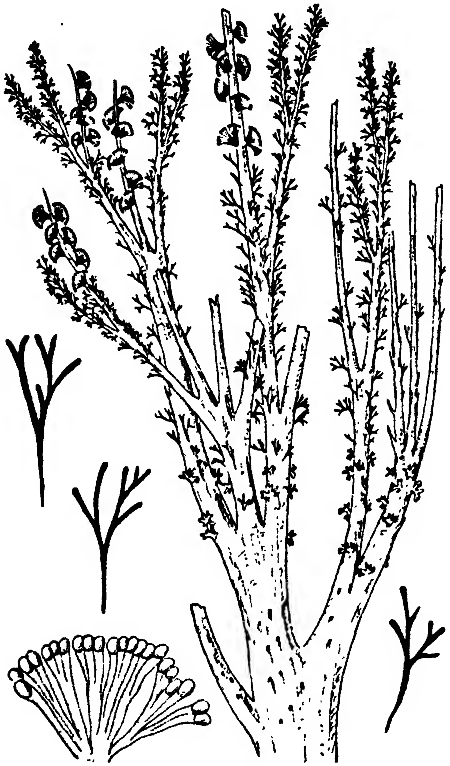


Fig. 1026. ***Cladoxylon scoparium*, a mid-Devonian pteridophyte related to the fern stock**

This specimen has fan-shaped fertile leaves with sporangia, and small divided sterile leaves

Devonian Period

Early Devonian. A very great change in the flora of the world took place in the Devonian. Fossils of the oldest known land plants are found in the lower Devonian, and before the end of the period there had already developed a considerable diversity of terrestrial forms. The lower Devonian was the age of *Psilophytales*, which, as we have noted, are a very primitive order of the *Pteridophyta*. The *Psilophytales*, which we know, appear to represent a very generalized group of pteridophytes from which the higher orders of *Pteridophyta* diverged, and from which the seed plants are descended. In the earlier part of the Devonian the *Psilophytales* were widespread over the surface of the earth. They must have formed a strange type of low vegetation from which trees or even bushes were lacking.

Middle and late Devonian floras. During the middle and latter part of the Devonian we see great advances in the structure of

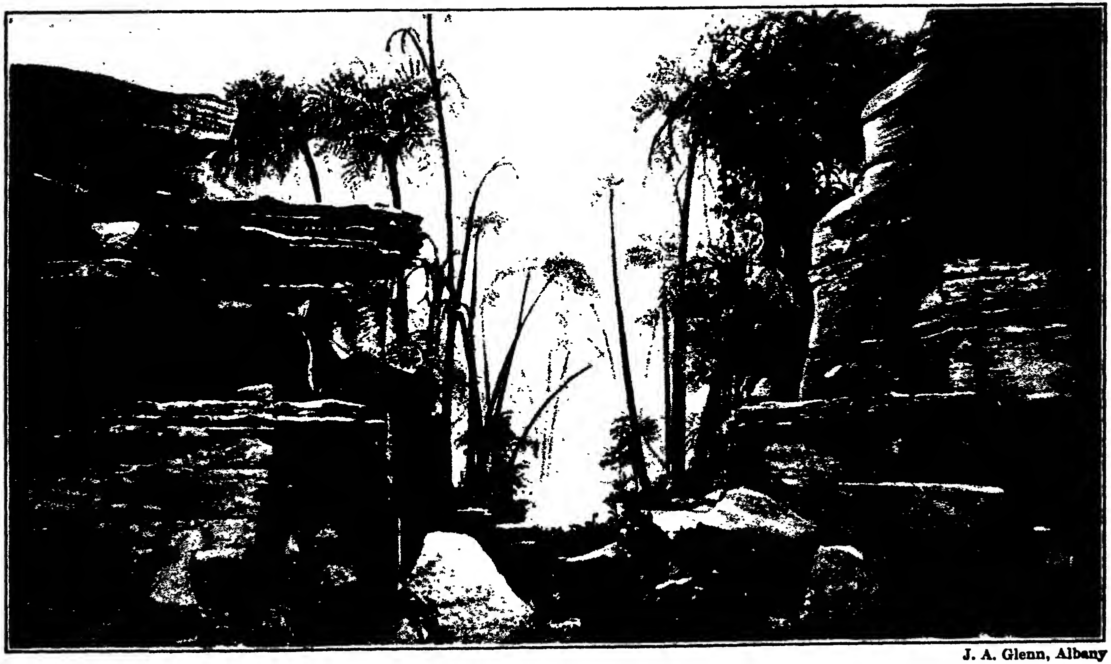
 J. A. Glenn, Albany

FIG. 1027. Restoration of a late Devonian forest of New York

The trees are *Protolepidodendron primaevum*, a lycopod, and the seed-fern *Eospermatopteris textilis*. In the foreground are seen actual stumps of the latter species. (After Goldring. Courtesy of the New York State Museum) plants, and the coming in of various new types. These appear to have been derived from the *Psilophytales* of the earlier Devonian times. There were primitive *Equisetales* and also ferns of a primitive type.

In the upper Devonian of New York there have been found abundant remains of a seed-fern with large fronds which, when living, is believed to have been a tree ten or twelve meters tall (Figs. 952, 1027). The seed-ferns, as we have seen, are the most primitive of the seed plants, and indicate a common ancestral stock for ferns and seed plants. In the upper Devonian of New York we find also a large lycopod (Figs. 1027, 1028). This was a tree probably twelve meters in height, a forerunner of the giant lycopods of the Carboniferous.

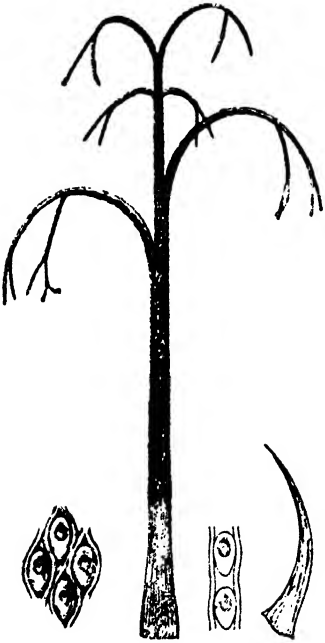


FIG. 1028. ***Protolepidodendron primaevum***

Lower left, aerial leaf scars on upper part of stem; lower center, arrangement of leaf scars on lower part of trunk; lower right, a leaf. (After Berry)

The two great lycopod genera of the Carboniferous period were *Lepidodendron* and *Sigillaria*. In *Sigillaria* the leaf scars are arranged on ribs in vertical rows, while in *Lepidodendron* they are in spirals. In the Devonian lycopod (*Protolepidodendron*) they are in vertical rows at the base of the plant and are more or less spirally arranged on the upper parts.

Before the close of the Devonian there was a great variety of pteridophytes. These included the lycopod genus *Lepidodendron,* which became so prominent in Carboniferous time; also the genus *Sphenophyllum* of the *Equisetineae.* The various plants from the middle and upper Devonian forecast groups which were prominent in the Carboniferous period (Fig. 1037).

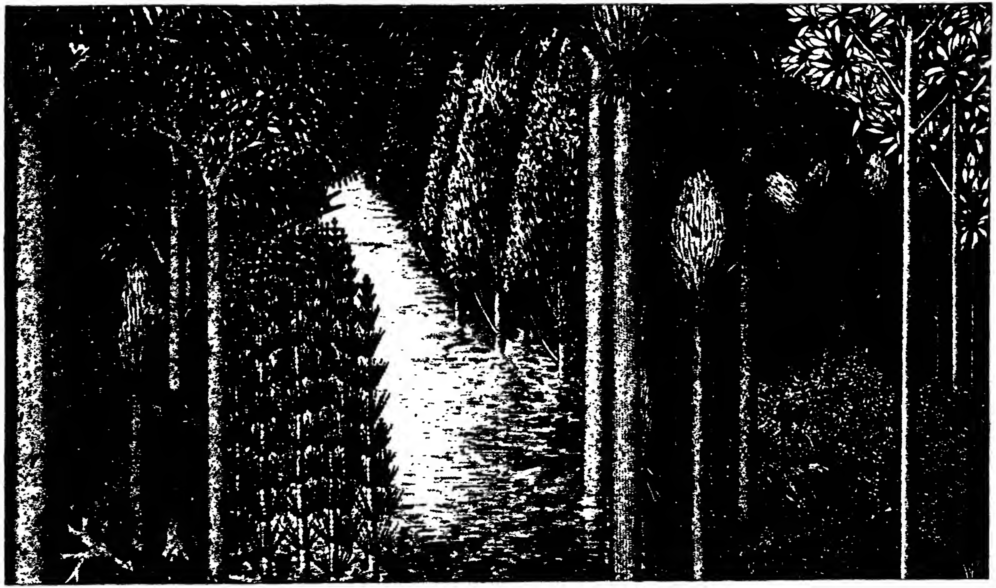


FIG. 1029. Generalized reconstruction of a Carboniferous forest

The tall much-branched trees to the left are *Lepidodendron*. Below these are *Sigillaria*; one is branched once and one is unbranched. In among the trunks are leaves of *Lyginopteris*. A small lycopod is growing on the fallen *Sigillaria* trunk. In the center foreground is a slender type of calamite and in the background two much-branched tree types. To the right of the water are a number of *Sigillaria*, also a tree fern. In the extreme right is a group of *Cordaitales*. In the undergrowth are several *Cycadofilicales*. Among those in the extreme right is a *Sphenophyllum*

Carboniferous Floras

Environment of Carboniferous period. Very favorable conditions for the growth of plants were widespread during the Carboniferous period. A uniform mild, perhaps subtropical, climate seems to have extended north into the Arctic regions, as the same plants, of tropical appearance, are found in America, Europe, and within the Arctic circle. There were vast plains from which the water drained but slowly, and so there were great fresh-water swamps, in which were laid down the tremendous Carboniferous coal beds. The vegetation which gave rise to these immense beds of coal has been regarded by many geologists as one of the most luxuriant which have been recorded in geological history.

In North America the deposits of the lower and the upper Carboniferous are so distinct that American geologists usually separate them into two periods, the earlier called Mississippian and the latter Pennsylvanian. The Pennsylvanian was the period of the great coal beds. For the sake of simplicity, and because it is often difficult to distinguish between Mississippian and Pennsylvanian floras, these two periods are here regarded as constituting the Carboniferous period.

Plants of the Carboniferous period. Prominent among the plants of the Carboniferous period were giant horsetails (*Equisetales*) and lycopods (*Lycopodiales*) (Figs. 913, 1029). The horsetails reached a height of twenty or thirty meters and a diameter of a meter, and the lycopods attained even greater dimensions. Ferns were rather scarce, but seed-ferns (*Cycadofilicales*) were exceedingly abundant. Most of the latter were relatively small, although some may have been fair-sized trees. An extinct order of tall gymnospermous trees (*Cordaitales*) was conspicuous, and there is evidence to indicate that the conifers made their appearance before the close of the period (Fig. 1030). More than two thousand species have been recorded from the Carboniferous period, and it is not probable that we are acquainted with half that actually existed.

Carboniferous forests. The vegetation of the Carboniferous period varied from place to place as does modern vegetation. It also underwent changes as time passed. We cannot, therefore, give a description which would fit all of it. However, we can picture, more or less, the plants which in various combinations made up that vegetation.

The tall trees, about thirty meters in height or taller, were lycopods (particularly *Lepidodendron* and *Sigillaria*), *Calamites*, and *Cordaitales*. Not all of the lycopods and calamites were such giants; many of them were smaller plants, and among the lycopods were small herbaceous species similar to *Selaginella*. Less lofty than the giant lycopods and calamites were the tree ferns of the late Carboniferous and Permian periods. Among the smaller or medium-sized plants, seed-ferns were very conspicuous, while ferns were present. Slender sphenophyllums probably scrambled over the other plants.

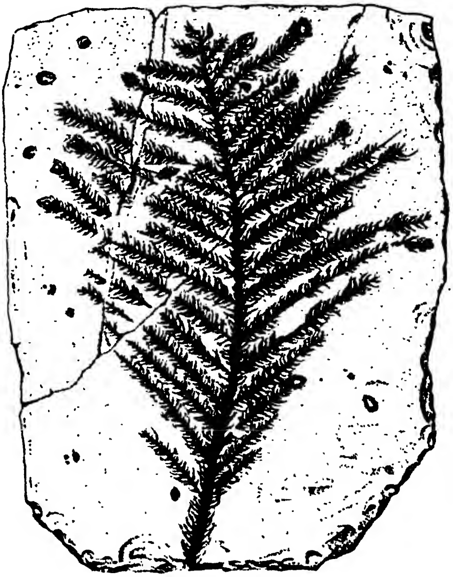


Fig. 1030. *Walchia frondosa*, one of the Paleozoic *Coniferales*

After Renault

Ferns. Most of the fernlike fossils which are so abundant in the Carboniferous period have proved to be seed-ferns (*Cycadofilicales*). In other cases it is not known definitely whether they are true ferns or seed-ferns. However, there is one large class (early ferns, or *Primofilices*) which appear to be certainly of fern stock. They were small plants of an ancient race extending back into the Devonian period. In most forms of the early ferns (*Primofilices*) the fronds apparently consisted of naked rachises on which the sporangia were borne terminally.

THE CLOSE OF THE PALEOZOIC ERA

The Permian is the last period of the Paleozoic era. The Carboniferous grades into the Permian gradually, and there is much question as to whether certain stages of development started in the late Carboniferous or in the early Permian. It is therefore more convenient not to try to define too exactly what is here regarded as the closing epoch of the Paleozoic era.

Geological changes. In late Paleozoic times there was active mountain building and a rearrangement of large areas of land and sea. At this time the Appalachian as well as other mountain chains elsewhere were raised to great heights. In the southern hemisphere there was widespread glaciation in an ice age severer than the more familiar Pleistocene ice age; dryness and coldness became widespread, and there was a great impoverishment of the flora.

Changes in flora. The changes in vegetation which mark the close of the Paleozoic came on gradually, but before the end of the Permian they were very profound. The giant lepidodendrons and sigillarias had disappeared, though small forms resembling *Lycopodium* and *Selaginella* continued into the Mesozoic period. *Sphenophyllum* and the true calamites seem to have become extinct; henceforth the *Equisetales* were represented by humbler types than the giant calamites of the Carboniferous. Ferns were abundant in the Mesozoic era, but many of the Paleozoic types, including the Carboniferous and Permian tree ferns, disappeared by the close of the Paleozoic, and many of the Mesozoic ferns were more recent types. Many of the prominent *Cycadofilicales* died out, but the order continued into the Mesozoic with greatly decreased importance. *Cordaitales* are not known to have survived the Paleozoic, but leaves similar to theirs have been found in Triassic strata. Altogether, it may be said that the plants which dominated in Carboniferous times had practically passed away before the close of the Paleozoic era.

While the late Paleozoic saw the passing of many types of plants, new ones belonging to the *Cycadales*, *Ginkgoales*, and *Coniferales* had come upon the scene. These orders, together with new types of ferns, were destined to dominate the greater part of the Mesozoic era.

***Glossopteris* flora.** While in earlier Carboniferous times there were similar floras in both northern and southern hemispheres, a very distinct flora developed in the south during the late Paleozoic. At that time there was a great southern continent, known as Gondwana Land, which embraced much of Australia, India, Africa, South America, and Antarctica.

A sea separated what is now eastern Asia from western Europe, but across the North Atlantic there was a land bridge, and also one from Africa to South America.

Gondwana Land was separated from the northern lands (Europe and most of Asia) by the Tethys Sea. In Gondwana Land there occurred what was perhaps the most severe glaciation of geological history. In this region there developed also a very distinct flora, called the *Glossopteris* flora from the genus *Glossopteris*, one of its prominent constituents (Fig. 1031). The dominant plants had large, coarse fernlike leaves, some of which, including *Glossopteris*, were entire. These plants are believed by many to have been seedferns. The *Glossopteris* flora was much poorer in species than the forests contemporary with it in the northern hemisphere, but it contained species belonging to all the great orders of Carboniferous plants.

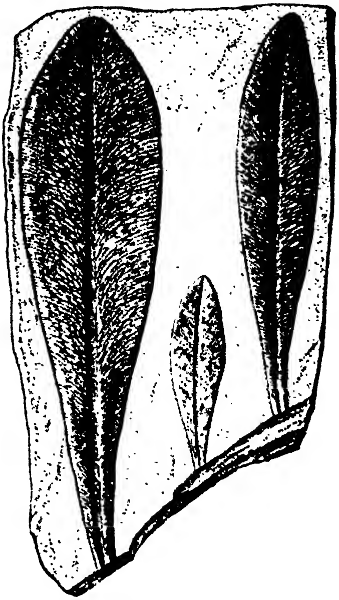


FIG. 1031. *Glossopteris browniana*

After Brongniart

Before the close of the Permian there must have been some land connection across the Tethys Sea, as Gondwana plants migrated to the northern continent. As these hardy forms and their descendants spread, they produced great changes in the character of northern floras.

MESOZOIC FLORAS

Triassic. In the earlier part of the Triassic period the climate continued to be generally drier and less uniform than before the Permian glaciation. Plant fossils from the earlier Triassic are scarce. The vegetation was probably not so rich as in the Carboniferous. However, some of the apparent scarcity may be due to the fact that the conditions under which the sedimentary rocks of the period were formed were not favorable for the preservation of vegetable remains. We have more plant fossils in rocks of the late Triassic, when the passage of time and the stimulus of changed conditions had resulted in a vegetation very different from that of the early Permian.

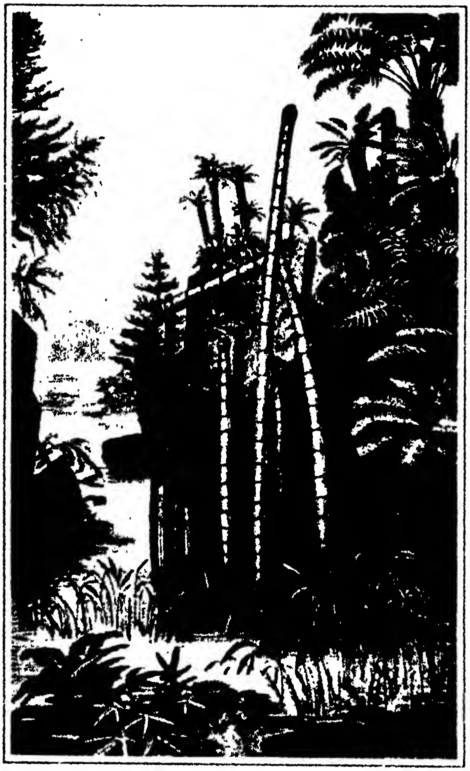


Fig. 1032. A Triassic landscape

After Heer

Relatives of the great groups of the Paleozoic era lingered on in the Triassic. The *Equisetales* were represented by forms much smaller than the giants of the Carboniferous and intermediate between them and recent species (Figs. 868, 1032). By the end of the Triassic the larger forms had disappeared, leaving only smaller ones comparable with those of today. The same is true of the *Lycopodiales*. The position of the seed-ferns is obscured by the difficulty of distinguishing between seed-ferns and true ferns. However, this line appears to have been carried on far into the Mesozoic by forms different from those which were prominent in the Paleozoic.

Dominant plants of the Mesozoic period. From the Triassic to the lower Cretaceous the flora was dominated by *Ginkgoales*, ferns, conifers, and particularly by cycadophytes (cycads and their relatives).

Ferns. The ferns (Figs. 1033–1035) attained only moderate dimensions. They were more abundant than in the Paleozoic era, though probably somewhat less so than at present; and they represented more modern types than did the Paleozoic forms However, families which were common and widespread in the Mesozoic have since dwindled in importance, while other families have risen to greater prominence.

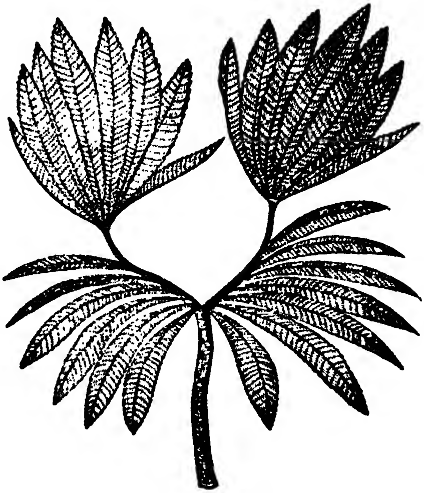


Fig. 1033. *Clathropteris*, a Triassic fern. (× ¼)
After Berry

Trees. The trees of the Triassic and Jurassic were conifers and *Ginkgoales*. Conifers were numerous and widely distributed; probably, however, the commonest trees belonged to the *Ginkgoales*. In the Mesozoic there were several genera and numerous species.

The Cretaceous period and the coming of angiosperms. The first definitely known angiosperms, other than the *Caytoniales*, are found in the earlier part of the Cretaceous period. Some petrified stems of angiosperms found in the lower Cretaceous are thoroughly angiospermous in anatomy without any trace of gymnospermous characters. Moreover, different specimens show considerable diversity in structure. The sudden appearance of angiosperms during the Cretaceous in great variety of forms leads to the belief that they must have undergone a long period of evolution before the time at which they come to our notice. Other than the presence of the *Caytoniales* in the Jurassic, there are very few and inconclusive direct indications of the presence of angiosperms before the Cretaceous.

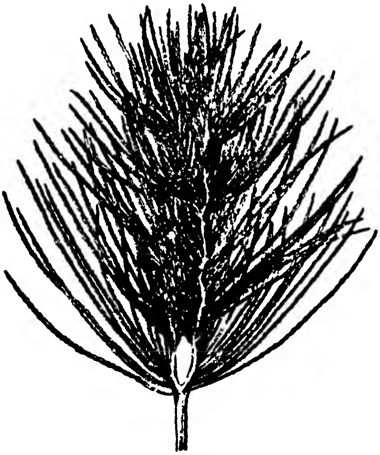


Fig. 1034. ***Camptopteris spiralis*, a Triassic fern.** **(× ⅛)**

After Nathorst

There is evidence that a considerable part of the evolution of the angiosperms took place within the Arctic Circle. Early in the Cretaceous a varied dicotyledonous flora occurred in Greenland along with older types. Similar dicotyledonous floras, which appear to have migrated from such a center, are found later in Asia, North America, and Europe. During Cretaceous times there was a southward spreading of floras in Asia, North America, and Europe which reached as far as South America and Antarctica.

Before the end of the lower Cretaceous, angiosperms were a prominent element in the flora. By this time a number of modern families and genera were represented.

Among the families found in Maryland and Virginia from the upper portion of the lower Cretaceous are such as the willow (*Salicaceae*), beech (*Fagaceae*), elm (*Ulmaceae*), fig (*Moraceae*), celastrus (*Celastraceae*), grape (*Vitaceae*), laurel (*Lauraceae*), soapberry (*Sapindaceae*), and water-lily (*Nymphaeaceae*) families.

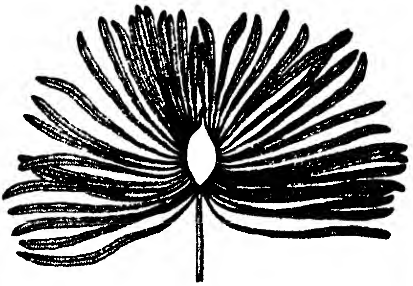


Fig. 1035. ***Dictyophyllum exile*, a Triassic fern.** **(× ⅓)**

After Nathorst

Upper Cretaceous. In upper Cretaceous times angiosperms were the dominant plants. Before the close of the Cretaceous monocotyledons had begun to appear.

During the Cretaceous a mild uniform climate seems to have been widespread, as the same floras occur in North America, Europe, Asia, and Greenland. In the latter place temperate-zone plants (poplars, walnuts, magnolias, pines, oaks, etc.) occur along with tropical types (breadfruit, figs, cinnamons, etc.).

In upper Cretaceous times new angiosperms continually appeared and older types disappeared. Before the close of the period most of the archaic plants of former floras had become extinct. The cycadophytes and *Ginkgoales* had lost their dominant place, most of their types had disappeared, and henceforth they were to be represented by remnants which would occupy only insignificant places in the floras of the world. Their position was similar to that of the lycopods and horsetails after the passing of the Paleozoic. The *Ginkgoales* came very near to sharing the fate of the *Cycadofilicales* and *Cordaitales*.

CENOZOIC VEGETATION

Before the close of the Cretaceous period, angiosperms had become the dominant group of plants; and they have so continued until the present. Many living genera were represented at the beginning of the Cenozoic era, and the flora had a very modern aspect. However, herbaceous species were much less abundant than at present, and individual species of plants had a much wider distribution.

The floras of temperate North America and central and western Europe were such as are now characteristic of more southern regions, and contained numerous tropical genera, thus indicating a warmer climate (Fig. 1036). A more temperate flora occurred from the Ural Mountains across Siberia to northern Japan. A luxuriant temperate flora flourished in Greenland.

The climate of the southern hemisphere appears to have been more similar to that of today than in North America and Europe, and no such great changes have occurred since as in the latter localities.

The Pliocene period saw a general cooling of North America and Europe, and the vegetation became more like that of today.

During the Pleistocene, great ice caps reached over much of North America and Europe. They did not spread out only once, but several times alternately spread and then retreated. When the ice spread, plants were forced to migrate; and when it retreated, vegetation followed. In North America as the ice extended south there were relatively easy routes of migration for the plants, which could return when glaciation had passed. The same was true in eastern Asia, and the result of this was that many of the widely distributed plants of the early Cenozoic persisted and that the floras of eastern Asia and of eastern North America have many points in common. This resemblance is seen not only in many genera but even in numerous identical species. Thus the tulip tree, the bald cypress, and the sassafras are common to the two regions.

FIG. 1036. Switzerland in Miocene times

After Heer

In Europe conditions were different. The high mountains across southern Europe, themselves capped with glaciers, and the seas to the south of them formed an effective barrier against the migration of many species, especially the more tropical ones. Thus many species perished, often not to return to this continent. To a considerable extent Europe had to be repopulated after the ice age, probably mostly from central Asia.

Another effect of the ice age is seen in the occurrence of arctic types high up on isolated mountains. As the ice spread south, so did arctic plants. When the ice retreated north, the plants followed; but they also followed the glaciers as they retreated up the mountains, and they then became isolated.

While angiosperms have dominated throughout the Cenozoic, there have been many changes in the kinds of plants and their distribution. Old types have disappeared, and new ones have taken their places. Forms which were important and widespread have dwindled, while others less prominent have increased in abundance and become widely distributed.

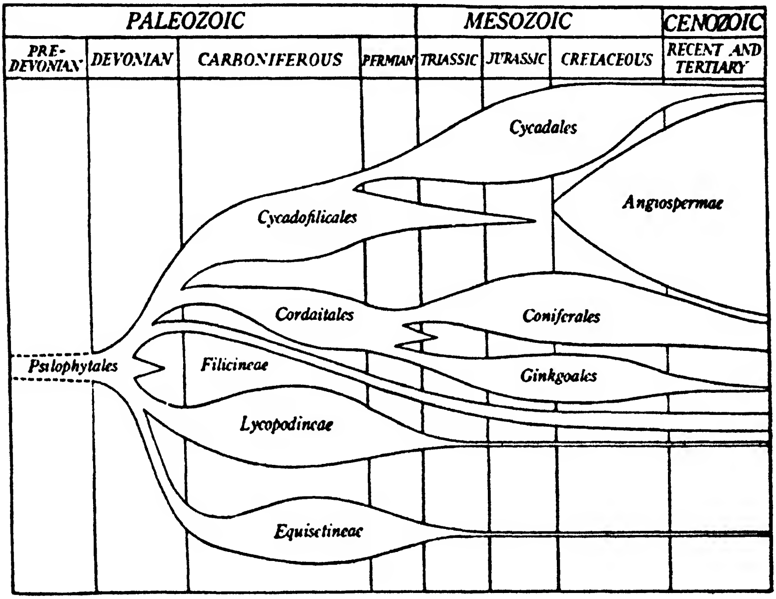


Fig. 1037. Diagram of distribution and importance of orders of *Pteridophyta* and *Spermatophyta* in geological time

The relationships of the different orders are also indicated

The dwindling importance of certain conifers during the Cenozoic has been very striking. The bald cypress, now of limited distribution, once flourished over much of North America, Europe, and Greenland. The genus *Sequoia* was once prominent over much of the world.

CONCLUSION

Throughout geological time there has been a continued succession of plants. The opening chapters of geological history show the presence of only the simplest forms. With each era, and, where we know the details better, with each succeeding period or portion of a period, more complex and highly evolved plants made their appearance. They became dominant, only to be superseded later by newer and more progressive groups. Fortunately for our understanding of them, ancient plants which have given way to more advanced ones have often left fossil remains or living representatives or both; and these enable us to reconstruct much of the history of the plant world (Fig. 1037).

In the early part of the record we see the successive appearance of higher types, but the details are hazy. Beginning with the Devonian, the picture becomes much clearer. Not only are the plants of succeeding times more advanced than their predecessors, but predecessors and successors grade into each other to such an extent that there seems to be no doubt that the newer plants were derived from the older ones through a process of gradual change. This gradual development is called evolution. The net result is that there has been evolved a flora which is wonderfully suited for the needs of man; and so, without implications of any kind, it will not be amiss to end this chapter with the following quotation:

> 11. And God said, Let the earth bring forth grass, the herb yielding seed, and the fruit tree yielding fruit, after his kind, whose seed is in itself, upon the earth: and it was so.
>
> 12. And the earth brought forth grass, and herb yielding seed after his kind, and the tree yielding fruit, whose seed was in itself, after his kind: and God saw that *it was good*.
>
> Genesis I. 11, 12.

CHAPTER XXX

EVOLUTION

The production of anything by the process of gradual unfolding or gradual change is known as evolution. In this sense we speak of the evolution of a machine, the evolution of civilization, the evolution of a nation, the evolution of the world, or the evolution of the universe.

The present configuration of the earth is known to be due to the accumulation of the same kind of gradual changes as are going on around us at the present time. Streams gradually deepen their beds; soil is washed from hillsides into rivers and then carried into lakes or seas; in this way the earth has become cut into ridges and valleys. In some places the land is rising, while in others it is sinking. Earthquakes and volcanic eruptions also modify the geography of a locality. Changes such as those mentioned have evolved the present configuration of the earth's crust.

Plants and animals also undergo change; and a study of the origin of cultivated plants shows that most of the varieties have been produced by the selection of desirable variations. The wild species that inhabit the earth at present are also derived from previously existing plants. Such species are continually under the influence of natural selection. When a favorable mutation occurs in either a plant or an animal, there is a tendency for individuals having this mutation to persist at the expense of those without it. In this way the flora and fauna of the earth are gradually undergoing changes which tend to fit them better to the environment. This process is naturally a slow one. Animals and plants are already very thoroughly fitted to their environment, and it is not to be expected that changes which would make them more so would be conspicuous during the lifetime of one man.

The evolution of plants and animals, or the accumulation of the gradual changes which occur in them, is known as *organic evolution*.

Organic evolution. According to the theory or law of organic evolution the present floras and faunas of the world have been derived from those of past ages by gradual changes. During the course of these changes the organisms have, in general, become more complex and better fitted to their environment. The gradual process of evolution has, moreover, evolved plants and animals that are suited to very diverse environments. The original ancestors of present-day plants and animals must have been very simple indeed as compared with the most complex of their modern descendants.

The general similarity of protoplasm in physical structure, chemical composition, and physiological responses certainly indicates that all protoplasm came from the same source. Moreover, the similarity of the phenomena of sexuality and inheritance argues for a relationship of all higher animals and plants.

Evidence of change. In connection with the evolution of plants there are two main questions which require consideration. First, are the plants of our present flora the result of a process of evolution? Second, assuming that they are, what has been the nature and cause of this process? We will first consider the proof that evolution has taken place in plants.

Plants at the present time undergo mutation; in other words, they change. We have seen that these mutations are due to changes in chromosomes and that the characters which result from mutations are inherited in Mendelian fashion. This proves at once that organisms can change or undergo evolution.

We next have to determine the extent to which they may evolve or have evolved. Fossil records, comparative morphology, and geographical distribution are probably the most important lines of evidence for evolution in plants; and one can realize the completeness of this evidence only after making a thorough study of these subjects. The evidence for evolution is not, however, confined to these, as all the fields of biology afford striking evidence. The more one knows of biology the more complete the evidence becomes.

Geological evidence. In previous chapters we have traced the record of fossil plants from very early times to the present. In the last chapter the evidence was summarized. It showed that in very early times the plants were exceedingly simple, and that as time passed they become more and more complex until finally the present very highly developed floras appeared. We also saw that the plants of one age or period graded into those of the next in such a way that the only reasonable explanation was that the plants of one age were derived by gradual change from those of the preceding age. In other words, there has been an evolution of plants throughout the long ages covered by the fossil record.

Comparative morphology. When one examines the plants we know, both living and fossil, and tries to arrange them in an orderly sequence, he comes to exactly the same conclusion as he does from a consideration of the fossil record. This we have already learned.

The most complex plants are characterized by having flowers and a complicated method of reproduction. Plants show many gradations, from single-celled plants without sexuality to the complex condition found in flowering plants. In some simple single-celled plants there is a fusion of similar cells ; in such cases there is no differentiation of sex. In various lines we have traced the evolution of sex. Some slightly higher types show an indication of the differentiation of sex. In more advanced forms there is a fusion of large and small gametes, while in still more progressive types there is a fertilization of eggs by spermatozoids. Between the simplest plants with eggs and spermatozoids and the flowering plants there are still many gradations of complexity in sexuality.

Just as there are gradations in the development of sexuality, so also there are gradations in vegetative complexity. There are single-celled plants which not only lack sexuality but do not have a well-defined nucleus, and in which the photosynthetic coloring matter is diffused through the protoplasm instead of being contained in special plastids. In somewhat more highly developed types the whole plant consists of either a single cell or a group of similar cells with well-developed nuclei and chloroplasts. Between this simple vegetative structure and the differentiation characteristic of flowering plants there are many gradations.

When we try to classify the various plants we find that they naturally fall into classes, the members of a class being alike in that they have certain common characteristics and differing from plants of other groups in that they possess characters not found in those groups or lack characters which those possess. In classifying the members of a group it is natural to arrange them from the simplest to the more complex. When we do this and then try to arrange each group near to the groups which it is most like, we find that the whole system of classification takes the form of a branching tree (Fig. 1038). Thus, the various higher orders of gymnosperms point back to the *Cycadofilicales*, and the *Cycadofilicales* to a fernlike stock; in the *Pteridophyta* we see a converging toward the *Psilophytales*; in the green algae the three main lines of evolution converge toward a single-celled motile type such as *Chlamydomonas*. Comparative morphology and classification therefore indicate, as does paleobotany, that our present plants are the result of evolution, which in general has been from the simple to the more complex, and which during the course of time has produced a radiating development resulting in a great diversity of forms.

In plants we find many structures which can be best explained as survivals from past ancestors. In the green algae, liverworts, and pteridophytes, fertilization is by means of motile spermatozoids; and in these plants the motility is very useful in enabling the spermatozoids to reach the eggs in the archegonia. The presence of flagellated spermatozoids in the simplest of the living seed plants, where the spermatozoids are carried to the archegonia by pollen tubes, can certainly be best explained as the survival of an ancestral characteristic. Perhaps equally striking is the occurrence of prothallial cells in the male gametophytes of *Selaginella*, *Cycas*, and *Pinus*. Also noteworthy is the presence of the very evanescent ventral canal cells in *Cycas* and in *Pinus*. The ventral canal cell, in such cases, can be best interpreted as a remnant of the row of neck and ventral canal cells seen in liverworts and homosporous pteridophytes, where it serves a real function in opening a way for the spermatozoid to pass through on its way to the egg. Very many such cases of relics are known in the plant kingdom.

During their embryology plants often go through stages which indicate relationships. Many of these are too technical for present considerations, but some are quite striking. Leaves of many species of acacia are pinnate. In Australia, where acacias are very common, there are a number of species, growing under very dry con-

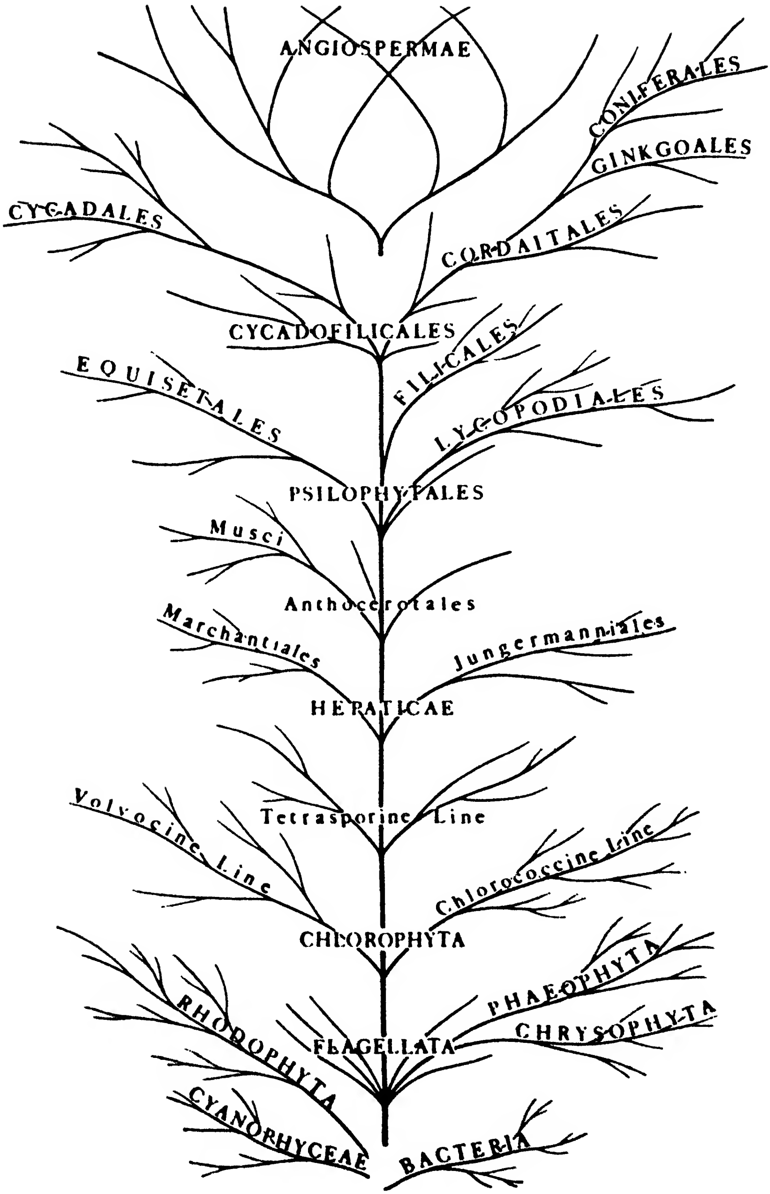


Fig. 1038. Diagram indicating systematic arrangement of different groups of the plant kingdom

This diagram suggests probable or possible relationships ditions, whose leaves are highly modified in that a mature leaf has no blade, but the petiole is flattened and modified into a leaflike structure known as a phyllode. Acacias of this type show that they have been derived from the ordinary type of acacia because the first leaf after the cotyledons is pinnate and similar in structure to the seedling leaves of an ordinary acacia (Fig. 1039). Sometimes several leaves may be pinnate and there is a gradual change from the typical pinnate leaf to the phyllode condition.

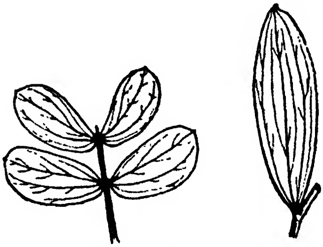


FIG. 1039. Leaves of a species of *Acacia*

On the left is the first leaf after the cotyledons; on the right is a somewhat older leaf in which the petiole is flattened and leaflike and takes the place of the leaflets. (× 1)

Geographical distribution. The present distribution of plants and animals can be explained only in the light of evolution.

Many plants have excellent means of seed dispersal and are very widely distributed. Frequently these are recent and very successful species and give us little or no insight into the past history of plants. In general, however, high mountains or seas impose barriers which many plants and animals cannot cross very readily if at all. Hence species or groups of related species are often confined to one area or to a limited number of separate areas, and it is these species that give us the greatest information concerning the origin of plants and animals.

From geological evidence we find that all the continents have had land connections in the past, and, moreover, that many land areas which at present are islands were formerly connected with continents or with other islands. The floras of different regions and islands frequently differ widely from each other, and in general this difference increases with the length of time during which the two areas have been separated from each other by barriers such as high mountains or seas. This is easily explained by the teachings of evolution. When there is communication between two contiguous areas, the plants and animals of the two areas are naturally interchanged. If later the two areas become separated, as by the submergence of land connections, the flora and fauna of each will continue their evolution separately. Owing to the method by which evolution takes place, it is not to be expected that the course of evolution will be the same in the two different localities, but rather that evolution will take place in a different direction in each. In this way the longer the two areas are separated the more distinctly different their faunas and floras become. Australia has been separated from the rest of the land areas of the world for long ages, and as a result its fauna and flora are strikingly different from those of the rest of the world. The great development of eucalypts (Fig. 1040) and marsupials in Australia is well known.

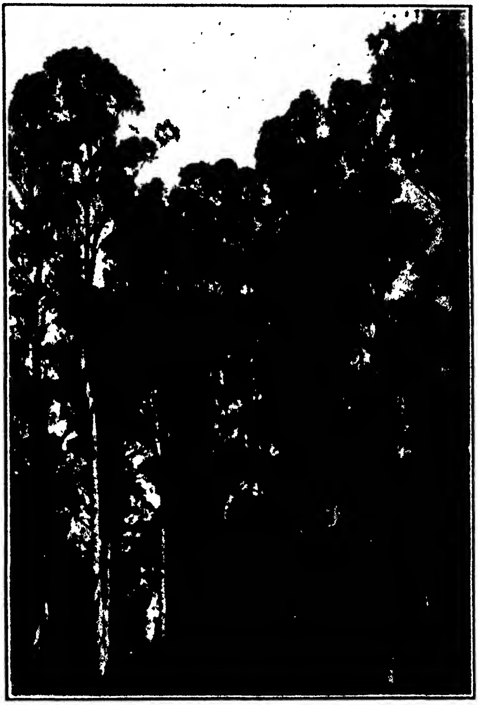


FIG. 1040. Eucalyptus forest of Australia

Photograph by Professor D. A. Herbert

Summary of evidence. We are now in a position to make a final summary of the evidence as to evolution. We have seen that the hereditary make-up of plants changes through mutations. Geological history, morphology and classification, and the geographic distribution of plants all combine to show that present floras are derived from those of the past through gradual change, and that there has been a development through evolution from a very simple beginning to great diversity and complexity. In other words, the evidence is that the plant kingdom, as we know it today, has been developed through the process of organic evolution.

Means of evolution. We have seen that the evidence shows that plants have developed through evolution; it now remains to inquire as to the causes and means of evolution. Here again the inquiry involves the answer to two questions. What has been the cause of the variations which have resulted in evolution, and what has preserved and accumulated these variations? We can answer the first question very simply by saying that the variations are the result of mutations, which are due to changes in the chromosomes. This much we know, and this subject has been considered in connection with heredity. The cause of these changes is a different matter, and we have already seen that our knowledge of this subject is in an unsatisfactory state. However, it has only been in comparatively recent times that we have realized that hereditary changes are due to mutations, or that we have found that mutations are due to changes in chromosomes. The cause of these changes is a subject of very great interest and active investigation at present. In the following paragraphs we will consider the means by which changes brought about by mutations have been conserved and combined in the evolution of plants.

Natural selection. The method of improving cultivated plants has been that of selection, which may or may not have been accompanied by hybridization. Not only is selection the method of improvement, but continued selection is frequently necessary if the best qualities of cultivated plants are to be maintained. Naturally all injurious mutations should be eliminated, as should all undesirable individuals resulting from hybridization.

Since selection plays such a prominent part in the growing of cultivated plants and domestic animals, it is not surprising that in nature too plants and animals are subject to a process of selection. This selection by nature is called *natural selection*, to distinguish it from artificial selection, or selection by man.

Struggle for existence. Observation of natural conditions indicates very clearly that, except where man has interfered, a given area contains about as many plants and animals as it can support. On the average, then, each plant produces one offspring which reaches maturity and takes the place of its parent. Every mature plant, however, produces many seeds, each of which contains a young plant. If all the seeds produced by one plant and its descendants should come to maturity, the descendants would soon be numerous enough to cover the earth. Likewise, if all the descendants of a pair of animals lived to old age there would be enough of them to populate the earth in a short time. Natural selection results from the facts that a given region is fully occupied by plants and animals, that these give rise to many offspring, and that, owing to competition, only a small proportion of the offspring can grow up and in turn leave descendants.

Owing to the large number of offspring produced, there is necessarily competition between the offspring and also between these and their parent. There is competition not only between individuals of the same species but also between different species. This competition is the so-called struggle for existence. In the case of animals it is perhaps easier to visualize than in the case of plants. There is, however, just as true competition between plants as between animals. Every farmer knows that it is necessary to keep down the competition between weeds and his crop plants by destroying the weeds. Otherwise the weeds would be successful and the crops would disappear.

Survival of the fittest. In the competition between plants and between animals chance plays a considerable part. For example, many seeds never reach situations where it is possible for them to germinate. Nevertheless it is true that in general those individuals that are best adapted to their environment and for withstanding competition will survive. In other words, competition results in the survival of the fittest. By this we do not mean the survival of those which are more pleasing or more useful to mankind, but those which are best fitted to live under the conditions of their environment and to withstand competition. The survival of the fittest might just as well be termed "the elimination of the unfit," as what really happens is that the unfit are eliminated.

In natural selection it is those plants that are not fitted to their environment or for withstanding competition that are eliminated, while in artificial selection the plants that are discarded are those thought to be least serviceable to mankind. It frequently happens, therefore, that mutations which would be selected and thus preserved by man are very different from those which are preserved by natural selection. Such a mutation as a seedless orange is desirable from the standpoint of man but could not continue to exist in nature. From the standpoint of a plant subject to natural selection, many seeds and a comparatively small amount of pulp are favorable characters.

In nature variegated leaves with white areas resulting from a lack of chlorophyll would be a disadvantage, as the material used in constructing these areas would be wasted as far as the chief function of the leaves is concerned. From the standpoint of artificial selection such plants are frequently desirable on account of their ornamental value. In nature such variegated leaves are very rare, but they are very common in cultivation.

Under natural conditions any mutation the result of which is unfavorable to the preservation of the species will be eliminated by natural selection, but there is a tendency for favorable mutations to be preserved.

From the foregoing discussion it is easy to understand why many of our cultivated plants cannot survive when left to themselves; it is also evident why plants seem thoroughly adapted to their environment.

Significance of sexuality. The value of sexuality is a subject about which there has been much dispute. All species of higher animals are composed of males and females. This results in the production of only half as many offspring as there would be if the animals were bisexual or reproduced by a vegetative process. The great majority of seed plants also reproduce sexually. Moreover, most of them are fitted with some device to insure cross-pollination. Considering that plants are subject to a rigorous natural selection, and that still the majority reproduce sexually, it would seem that this method must afford a real advantage.

Yet certainly neither cross-fertilization nor even a sexual process is necessary for successful reproduction. Among the lower animals there are bisexual species and also species in which the eggs develop without fertilization. Both these types of animals seem vigorous and successful. There are numerous seed plants in which a sexual fusion is unknown and which produce fertile seeds. This may result either from the development of eggs without fertilization or from the growth of a vegetative cell into the embryo sac and its subsequent development into an embryo. As has been previously pointed out, plants which are reproduced vegetatively or which are habitually self-fertilized seem as vigorous as those that are reproduced sexually.

While the sexual process is thus not necessary for successful reproduction, this method does afford great advantage in the production of variations upon which natural selection can act. If a favorable mutation appeared in an individual of a species and another favorable mutation in another individual, these two mutations could be combined only as a result of the sexual process. One advantage of the sexual process would seem to be the production of new types of individuals which may be better fitted to survive.

Course of evolution. From what has been said about the causes of evolution it will be evident that evolution does not follow a straight line; its course is a branching one. A diagrammatic representation of the course of evolution is therefore drawn as we should draw the branches of a tree, rather than as a straight line. Because one form has given rise to a second form it does not follow *that the first form will continue to exist unchanged or will ever* again give rise to that second form. The evidence from geographical distribution supports the idea that the evolution of a given form will produce different results in different times and places. When two regions with similar floras and faunas become separated, their floras and faunas develop along different lines, and the differences increase with the length of time the two areas are separated. We sometimes hear the question, If lower forms gave rise to certain higher forms in the past, why do they not continue to do so? In the first place, the ancestors of the higher forms are, for the most part, dead. In the second place, the evolution from one form to a very different form requires the combination of a great many circumstances acting through a long period of time, and it is not to be expected that all these conditions will ever exist more than once.

In view of the above, what is the relation between the simpler and the more complex plants that exist today? This question can be answered by a hypothetical example. We will start with a very ancient and simple plant which we will call *A*. We will suppose that this plant gave rise to two different forms, *B* and *C*, which were naturally very much like their parent *A*. *B* and *C* were better fitted to their environment than *A*, and in the course of time *A* died out and disappeared, while *B* and *C* both survived. *B* was very thoroughly adapted to its environment, and it continued to exist through long ages and is a component of our present flora. Either *C* was less fitted for its environment or for some other reason it underwent further evolution, so that it gave rise to form *D*, which in turn produced *E*, etc. As a descendant of *E* we have a living form, *X*, which is very different indeed from the parent form *A* and very much more complex. Now the relationship between *X* and *B* is clear. *X* is not a descendant of *B*, and *B* is very clearly not a descendant of *X*. *X* is, however, a descendant of *A*, which was very similar to *B*, so that we can say that, while *X* is not a descendant of *B*, it is a descendant of a form very similar to *B*. It seems very improbable that there still exist many, if any, of the forms of plants which were the direct ancestors of modern flowering plants, but it appears certain that many living forms are very similar to certain ancestral stages.

It does not follow that because a plant has a simple structure it is at a disadvantage as compared with more complex plants. Just as many trees are fitted for growing in the open, so many mosses are fitted for growing on trees, and many one-celled plants for floating in water.

Evolution and natural law. Organic evolution is simply the orderly working of a natural law. Just as a geologist studies changes in the surface of the earth brought about by the operation of natural law, and the astronomer contemplates the evolution of suns, solar systems, galaxies, and supergalaxies, so the botanist sees in the development of the plant kingdom the orderly working of the natural law of evolution. By unraveling the law of organic evolution the botanist has done much to make our useful plants still more useful. He has been so successful at this that he is in no small measure responsible for the recent great increase in the yield of agricultural products.

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